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ON THE FORAGING ACTIVITY OF THE WOOD ANT

BY S. J. HOLT

*Nature Conservancy, Edinburgh**

(With 7 Figures in the Text)

INTRODUCTION

The movement of animals in search of food is one of the primary causes of their dispersion over the area which a population comes to occupy. As such its study, as well as being of considerable theoretical interest, has potentially some practical importance. For example, these movements probably determine the average age at which young plaice (*Pleuronectes platessa*) appear on the main fishing grounds for that species in the southern bight of the North Sea. It seems that their general offshore displacement from the so-called 'nursery grounds' off the Dutch coast can be regarded as analogous to random diffusion in physical systems, at least until the basic pattern is modified by the onset of sexual maturity and the consequent highly oriented spawning migration during successive winters. Some of the problems arising from local movements in fish populations have been discussed elsewhere (Beverton & Holt, in press), special attention being paid to the attainment of steady-state distributions in a strictly limited area within which the distribution of food organisms and refuges was not uniform.

A detailed theoretical treatment of random dispersal has been given by Skellam (1951). The analytical model which he developed could be expected to apply even to some cases in which the behaviour patterns of the animals were 'such as to tend to lead them towards more favourable conditions'. One of the critical factors here is the particular time-scale used in the investigation, since dispersal which could be regarded as effectively random when measured over a period of years might be seen to be the cumulative effect of many processes, including non-random ones, if intervals of a day or week were used (see Beverton & Holt, in press). The search for food may be interrupted at intervals in order to rest and take shelter from enemies or the elements, and although this will not in itself materially affect the type of spatial distribution taken up by 'nomadic' animals, the foraging movements of species in which each individual returns continually to the same home base can be far from random.

The above usage is in keeping with Heape's (1931) distinction between a nomad, who 'shifts his home as he shifts his hunting ground, though at the same time he does not extend his wanderings beyond the boundaries of the territory which he regards as his own', and the animals which, though wandering within a given area, 'hunt from a permanent base. They possess a definite fixed home to which they always return'. The latter I shall refer to as resident species, but of course intermediate states between residence and nomadism must be recognized. In such species, especially those which are gregarious, depletion of the food supply near to the refuge

* Now with the Food and Agriculture Organization of the U.N., Rome.

by intensive hunting can lead to a rapid decline in the abundance of the population or to an invasion of adjacent areas, in which case the pattern of movement will be qualitatively altered. Overpopulation can, however, have slighter but chronic effects. Thus the contributors to a symposium on the effects of the fauna of nature reserves on the surrounding areas (International Union for the Protection of Nature 1952) confined their attention in effect to the problems arising when the animals which wander across an artificial boundary are a minority of the total population. The term 'drift' was used to describe such movements. It is generally recognized that in this situation the perimeter/area ratio is an important characteristic of a reserve, but relevant numerical data is sparse, and it was with this in mind that the investigation described here was undertaken.

Provided the habitat is not unduly changed by human interference or other agencies, nests of the wood ant often remain in one place for many years, and are associated with particular trees, the aphid populations of which provide in their excreta an important source of nutrients. It would be expected that under these conditions a relatively stable foraging system would be developed. Apart from its economic value as a predator on harmful forest insects (Gösswald 1951), this insect offers many advantages for the analysis of such a system. Identification and census are easy since each colony contains a large number of individual foragers which make and use clearly defined tracks, and from the foraging area (the 'trophoporic field') of which workers from other colonies are said to be excluded (Elton 1932). Also, food is not consumed on the spot but is brought back to the nest, so that the number of decisive contacts between predator and prey can readily be determined. For these reasons, and also because much experimental work has been carried out on the oriented movements of Hymenoptera, it was thought that wood ant populations would provide suitable material for a preliminary study of the economy of a gregarious resident species.

Workers from all the ant colonies described were kindly identified by Dr I. H. H. Yarrow of the British Museum (Natural History) as the species from Scotland previously known as *Formica rufa*, characterized by the possession of long hairs at the back of the head and a few long hairs on the mesopleuron.

THE SITE

Observations were made at various times between May 1951 and October 1952 of colonies—nests A and B—in a wood at Glen Coninish near Tyndrum, Perthshire (O.S. 1 in. Scotland, 62; 'Coille Coire Chuilc'). This relict of native pine forest on the lower northern slopes of Beinn Dubhchraig, 650–1000 ft above sea-level, has an area of slightly less than half a square mile and contains now at least fifty sizeable mounds, though Nelmes (1938) gave the number as twenty-one. They are confined to the middle of the wood, all being within 150 yd on each side of the burn Allt Coire Dubhchraig which runs through it, and they are constructed almost exclusively from needles of *Pinus sylvestris* L. subsp. *scotica* (Schott) E. F. Warburg, the dominant tree. Birches (*Betula* spp.) are also common and there are occasional rowans (*Sorbus aucuparia* L.).

A majority of the larger nests are on dry ridges with a southern exposure along

which run trackways—recognizable by an acid discoloration of the vegetable litter—radiating from the mounds and usually terminating at the foot of a pine or, more rarely, a birch tree. Owing to the rocky nature of the ground the tracks are in places very narrow where they pass between stones, and their boundaries near these constrictions are clearly defined. Very often they are forked, as described by Diver (1935), but I was unable to distinguish, as he could, between main and subsidiary roads, or to relate the traffic volume on a road to the number of trees served by it in any consistent way. Indeed, the greatest flow of foragers was frequently observed on a short but wide trail leading only to a small tree very near to the nest. Trees were rarely climbed on the side directly facing the line of approach, and on the few occasions that workers from two colonies used the same tree they invariably ascended on opposite sides of it. Where detailed observation of such cases was possible it was clear that the two streams explored different boughs of the same tree.

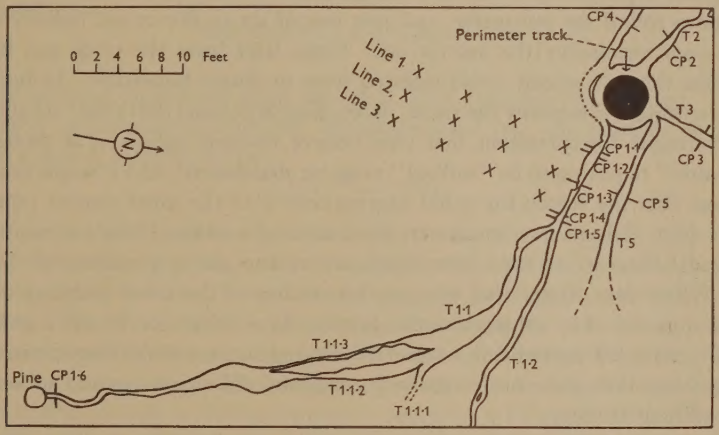

Fig. 1. Sketch map of part of track system of wood ant colony at Tyndrum, site A. Crosses mark places where measurements of density of foragers were made.

The most detailed census was made of colony A inhabiting a large isolated hill 5 ft in diameter and with a maximum height of 3 ft, although this height was reduced after heavy rain. A part of the track system associated with the colony is shown in plan in Fig. 1. No connexions could be traced between these roads and those of other mounds, although interchange of workers between parent and branch nests was fairly frequent in other parts of the wood. The only changes in this system observed during the period of the experiment were minor ones and arose from the fall of an old birch during the winter gales of 1951–2. Unfortunately the survey had not progressed far enough by that time for details of the effects of this event on the foraging distribution to be worked out.

THE FORAGING DISTRIBUTION

To a casual observer the activity of foragers outside the nest consists of a more or less ordered movement along the tracks. Outgoing and returning ants do not appear to move in separate columns, although when the tree is within about 10 ft of the edge

of the nest, and the trail to it is wide, incoming workers may tend to keep to the edges giving right of way to the unburdened ones. Closer inspection reveals the existence of a number of workers foraging in the sections between radii, and since they are rarely seen to leave the perimeter track encircling the mound by directions other than those of the recognized paths, it can be surmised that 'leakage' from these latter occurs, and at some distance from the nest. That the return journey is similarly an indirect one, in that successful foragers make first for a track rather than for the nest itself, may be inferred from the fact that whereas foragers at the distal end of a long trail were not often seen carrying insect prey, near the nest the proportion was higher. This could only have been obvious because a relatively small proportion of the prey was being brought down from the trees, but that is not perhaps the typical case, since, for example, Elton (1932) noted that very few insects occurred on trees with aphid 'farms' on them, and presumed that this was because of the depredations of ants.

The general picture is, then, that foragers leave the base of the mound at any point, move round the perimeter, and join one of up to five or six radially moving streams—not necessarily the nearest one. Some later leave the track and hunt for prey whilst the rest ascend aphid-infested trees to obtain honeydew. In both cases the return route is essentially the same. According to Nixon (1951) the 'old subjective and picturesque interpretation that ants behave towards aphids...as though they were "cattle" requiring to be "milked" must be abandoned', and it seems reasonable to suppose that the search for aphid aggregations is of the same general type as the hunt for prey. I have not, moreover, been able to confirm Elton's account of the specialized behaviour of some ants which are said to act as guardians of the aphid groups. When close observation was possible, mainly of the lower branches of rowan trees, it appeared that although under favourable weather conditions a group was practically never left unattended, none of the visiting ants remained there permanently, and only when that place was excessively congested did any arrive and subsequently leave it without feeding.

Rates of flow along a track were measured by counting the number of workers passing under a thread stretched across it at suitable places. For this purpose a click counter and a stop-watch were originally used, but later a simple manually operated recording instrument was developed that enabled data to be obtained more rapidly and made possible a complete census of the foraging activity of the colony in a short time during which environmental conditions were virtually constant. It was assembled by C. F. Palmer (London) Ltd., and consists essentially of a fan-governed clockwork recording drum with two-speed gear (one revolution in 30–60 s or 15–60 min) fitted with a set of six single-action electromagnetic signals with ink pens. One of these is actuated by a time clock giving impulses at 15 s or 1 min intervals, and the others by microswitches in a unit assembly connected to the equipment by 40 ft of multicore cable. A bell is set to give warning of the completion of a revolution of the drum, and the whole apparatus and a dry battery are housed in a wooden carrying case having room also for other small instruments, collecting tubes, spare pens, and so on.

With practice it is possible to record simultaneously the flow of ants in both directions and whether or not they are carrying solid food or waste materials in their mandibles. From the trace obtained both rates of flow and time intervals between

events can be measured. The accuracy of the latter is dependent primarily on the response characteristics of the recording pen and push buttons, but also on the reaction of the observer, constancy of drum speed (variation of order $\pm 2\%$) and errors of measurement. As used, intervals of 0·3 s could just be distinguished, but this was sufficient for the analysis of a moderately dense stream of ants.

A typical frequency distribution of time intervals between successive individuals passing a census point (CP) is shown in Table 1, where it is compared with the frequencies which would be expected if the flow was random, that is if the probability

Table 1. *Frequency distribution of time intervals between outgoing foragers. Callander, site C*

Interval (s) ...	0–1·9	2–3·9	4–5·9	6–7·9	8–9·9	10–11·9	12–∞	Totals
Observed number	54	23	14	9	3	1	2	106
Expected number (fitted Poisson)	50·4	26·4	13·9	7·3	3·8	2·0	2·2	106·0

Mean interval 3·1 s; flow about 19/min.

of an ant arriving during any short period of fixed duration was constant. Then the distribution of intervals would obey the exponential law, the number of duration between t_1 and t_2 being given by

$$N(e^{-mt_1} - e^{-mt_2}),$$

where N is the total number of intervals observed, m the reciprocal of the average interval length, and e the base of natural logarithms. The value of χ^2 for the frequencies given in the table, the last three cells being grouped together, is 1·6, with 3 degrees of freedom. The probability of such a discrepancy arising by chance is about 0·7 and it is therefore unnecessary for the present to regard the flow of ants along tracks as other than a random one. Similar conclusions have been reached regarding other types of traffic, including the movement of pedestrians (Tanner 1951). The flow of road traffic is very nearly random where the road is sufficiently wide to allow free overtaking without delays (Smeed & Bennett 1949). Where, however, the stream is at all congested, flow tends to be more uniform, as drivers are unwilling to approach closer than a certain minimum interval. Ants pass by climbing over obstructing individuals (both those moving slowly in the same direction and the opposing stream) as well as by going round them, but a comparable ordering effect may be observed, for example, where a small fallen branch or twig is used as a bridge to traverse a boggy patch of ground, and movement is thus impeded. Again, even though aircraft fly to a time-table, the accumulation of small errors in timing is sufficient to make the arrivals at a large airport effectively random (Bowen & Pearcey 1948).

The flow of foragers at site A along track T 1 (Fig. 1) was studied in some detail. This track led to the base of an old pine 45 ft high at a horizontal distance of about 60 ft from the nest centre and 30 ft below it. Although wood ants appear to differ from man and some other mammals in that their established tracks, or at least the unbranched ones, usually follow more closely the shortest practicable route to their objective, this one was unusual, because although the shortest route would have been 63 ft from the mound edge to tree base, the actual track length was at least 8 ft more

than this, the first 10 ft before the junction being along an old man-made path which determined the initial direction (cf. Elton 1932). Considered in relation to the size of the animal which uses them, ant roads are very wide, and the small deviations from the theoretical direct line which occur within this width arise principally because ways involving a minimum of unnecessary vertical displacement are followed, e.g. along the top of an obliquely fallen pine needle. Similarly, men in making footpaths often tend to follow furrows and otherwise to avoid direct and uncomfortable assault of a slight gradient or series of obstacles (Bates 1950).

Table 2. *Flow per minute at Tyndrum site A; track T1, series 1*

Census point ...		1·1		1·3		1·4		
Direction ...		−	+	−	+	−	+	
Group	Batch							
1	1	52	40	39	56	52	48	
	2	47	59	52	54	45	45	
	3	56	42	46	45	42	47	
	4	54	40	57	48	39	51	
	5	46	50	49	51	49	50	
2	1	55	49	52	50	56	50	
	2	50	51	64	60	46	48	
	3	43	56	61	55	45	50	
	4	44	57	45	48	54	42	
	5	51	46	52	41	48	52	
3	1	52	53	53	51	46	57	
	2	53	47	51	54	54	54	
	3	51	60	50	51	50	48	
	4	41	48	46	57	51	48	
	5	61	47	50	52	45	54	
4	1	47	50	50	54	49	46	
	2	52	55	48	51	54	49	
	3	52	43	53	57	44	46	
	4	44	48	54	49	54	46	
	5	60	54	46	46	50	46	
5	1	46	46	50	52	54	42	
	2	60	54	39	52	56	50	
	3	54	50	54	47	55	51	
	4	43	43	53	55	51	50	
	5	62	52	48	57	51	47	
Mean		51·04	49·60	50·48	51·72	49·60	48·68	50·19
		50·32		51·10		49·14		
Mean/50·19		1·0026		1·0181		0·9791		0·9999

In Table 2 are given the rates of flow per minute in both directions (flow away from the nest is designated negative; towards it, positive) at census points 1·1, 1·3 and 1·4 at noon on a June day when the track temperature at CP 1·3 was 13·5–14·5° C, and the flow had apparently been steady for some time. A group of five batches, each of 1 min duration were counted at each point in turn, and this was repeated four times. No significant differences were found between negative and positive rates, and no trend during the counting period of 1¼ h. These findings are typical of censuses made within 2 or 3 h on either side of midday and when the weather is relatively unchanging; on days without rain showers and with the sky either nearly cloudless or completely

overcast. Summaries of six censuses made under these conditions, in late summer of 1951 and between late spring and October in 1952, are given in Table 3. Series 1 is that of Table 2; series 2 and 6 are means of fifteen counts of 1 min made alternately at each census point in threes and expressed as fractions of the grand mean for each series, direction being ignored. Logarithms of these ratios are plotted against distance from the edge of the nest in Fig. 2, and it is clear that they tend to decrease with increasing distance. The apparent rates of decrease, as measured by the slopes of the

Table 3. *Rates of flow on track T1, site A*

		Series number						
		1	2	3	4	5	6	Mean
Temperature °C	Initial	13·5	13·0	19·0	12·0	14·5	8·5	—
	Final	14·5	13·5	21·0	12·5	14·5	9·5	—
Average flow per minute in both directions		100·4	127·8	215·9	78·2	123·1	46·4	115·3
Ratio of flow past each census point to the average flow	CP 1·1 (2·5 ft)	1·0026	1·0249	1·0208	1·0466	1·0201	1·0181	1·0222
	CP 1·3 (6·0 ft)	1·0181	1·0116	1·0059	0·9724	0·9894	0·9802	0·9963
	CP 1·4 (10·0 ft)	0·9791	0·9637	0·9749	0·9811	0·9904	1·0022	0·9819
Slope of linear regression of flow on distance from nest		−0·0033	−0·0083	−0·0062	−0·0085	−0·0039	−0·0019	−0·0053

regressions given in the last column of Table 3, do not depend on the actual rate of flow; the logarithms of mean rates of flow for all series have therefore been plotted, and there is no evidence of significant departure from a straight line (heavy line of Fig. 2). Rate of flow as a function of distance is, then, given by

$$N_b = N_a \exp\{-k(b-a)\}, \tag{1}$$

where N_a and N_b are the rates of flow past points at distances a and b respectively from the nest, and k is a leakage coefficient taking, in this case, a value of 0·0053. Leakage, therefore, and also infiltration of returning foragers, is about 0·5% per foot of track.

If equation (1) adequately represents departure from the track it seems to imply that leakage is a chance process and that any ant, wherever it may be on the track, has a certain small chance of leaving it before it has traversed a given distance. Checks on the validity of the exponential law for extrapolation over the required range of distance, and on the calculated value of k, were obtained by observing the rate of flow near to where track T 1 reaches the foot of the pine. At this point, CP 1·6, the track is wide and diffuse and it was necessary to measure the flow by a sampling method. Counts were made, over 5 min periods at the beginning and end of series 2 and 5 (Table 4, 'Before' and 'After'), of the number of ants passing under a 6 in. thread stretched across the central portion of the track. Previous estimates showed that 29% of the foragers passing along that piece of track used the central 6 in. lane when the total rate of flow was of the same order of magnitude as that occurring in these experiments, and it was established in a separate experiment at site B, that the relative distribution across a wide track is effectively independent of the traffic density over a wide range of values. The mean of the flow rates past census points 1·1, 1·3 and 1·4 has been taken to correspond with a distance of 6·17 ft (the mean distance of

those points from the origin), and from equation (1) the expected value at CP 1·6 (70 ft) can be calculated thus:

$$N_{70} = N_{6\cdot17} \exp\{-0\cdot0053 \times 63\cdot83\}$$
$$= 0\cdot6663 N_{6\cdot17}.$$

It is, however, necessary to correct this figure for losses occurring at track junctions. About four times as many foragers use T 1·1 as T 1·2, and twenty times as many use

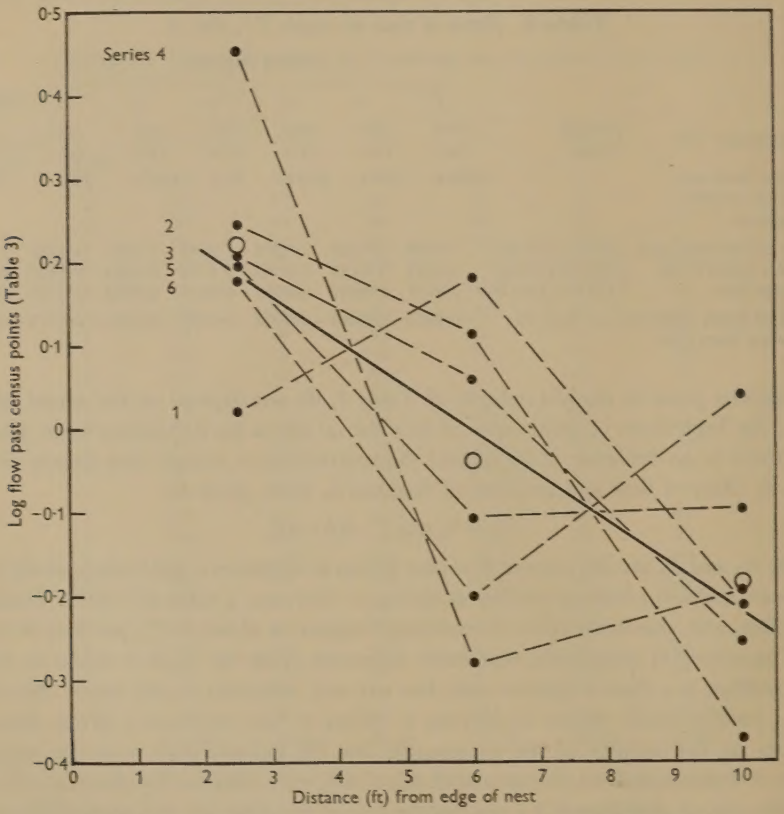

Fig. 2. Rates of flow of ants along track T 1 at site A, expressed as natural logarithms of the ratios given in Table 3.

the anastomosing T 1·1·2 and 1·1·3 as use T 1·1·1, so that the required proportion of the total using T 1·1·2 and 1·1·3 is the product $4/5 \times 19/20$. We therefore have:

$$\text{Expected} \quad N_{70} = N_{6\cdot17}\,(0\cdot6663 \times 0\cdot8 \times 0\cdot95)$$
$$= 0\cdot5064 N_{6\cdot17}.$$

The results are tabulated in Table 4 and the agreement between the observed and theoretical values (exponential extrapolation) is good, though when the approximate nature of the junction corrections is remembered it is clear that the smallness of the

differences, especially for series 2, must be due to chance. These figures, then, support the hypothesis of random departure. Before they were obtained it seemed likely that leakage from the distal half of the path would be higher than that from the first part as there the ground was steeper and more rough, and the trail less well defined, but there is clearly no evidence here to support this view.

Table 4. *Comparison of observed and theoretical flow of foragers at CP1·6, track T1, site A*

Series	$N_{6.17}$	Expected N_{70}: Exponential extrapolation	Expected N_{70}: Linear extrapolation	5 min counts at CP 1·6 (middle lane): Before	5 min counts at CP 1·6 (middle lane): After	Average per min/0·29
2	127·8	64·7	56·6	109	85	66·9
5	123·1	62·4	53·4	96	115	72·8

It follows from equation (1) that the proportion of ants reaching point 'a' which would be expected to leave the track between 'a' and 'b' is $1-e^{-k(b-a)}$. At various times a total of 347 workers, chosen at random, and travelling negatively between CP 1·1 and a narrow pass between two rocks 4 ft from it, were watched closely in order to obtain direct evidence of leakage. Of this number, eleven were seen definitely to leave the track and walk at least 6 in. from its edge, after which they were no longer followed. The expected number would be

$$347[1-e^{-(0\cdot0053\times4)}]=7\cdot3.$$

The probability of a discrepancy at least as large as this arising by chance, if the value of k used was the correct one, is about 0·16, so that no revision of the original hypothesis appears to be necessary.

Table 5. *Analysis of the behaviour of 347 outwardly bound workers for 4 ft after passing CP1·1, site A*

	Remained on track	Veered left	Veered right	Total
Burdened	1	0	1	2
Unburdened	335	6	4	345
Total	336	6	5	347

The data, subdivided according to which side of the track leakage was from and whether the forager was burdened with waste materials being brought from the nest or not, are shown in Table 5, and there is no suggestion that departure takes place much more frequently from one side than from the other. It is interesting to note, however, that the leakage of one burdened ant from the right-hand side was rather unexpected, since of the 347 that were watched only two were burdened, and, on the hypothesis that the behaviour of burdened and unburdened ants is in this respect the same, the chance of this happening is only

$$\frac{2\times10}{345}=0\cdot058.$$

In fact no workers carrying burdens negatively were seen to reach CP 1·6 during the period of observation. It was found that the number of burdened ants could be increased artificially by placing a small pile of barley grains, which seemed to be treated as if they were empty pupa cases, on the track near the nest. These were picked up by foragers leaving the nest, or very occasionally by returning ants—presumably already laden with honeydew—and carried away. Although this experiment was repeated several times, only once was a grain carried as far as CP 1·6 and subsequently up the pine tree and out of sight. Therefore the departure from the trail of a burdened worker either is a much more likely event than departure of an unladen one or it is not to be regarded as a chance process at all. Such departures, however, accounted normally for only about 1% of the total leakage between nest and tree.

Of the eleven ants seen to leave the path, six were taken back to CP 1·1 and gently placed on the centre of the track. Though rather disturbed by this, their behaviour suggested that particular ants do not leave the track at particular places. One of the six went back towards the nest; one, which had previously left the path on the left at 4 ft, left it on the right at 5 ft; the rest, after some hesitation in two cases, walked down the path as far as they could be followed—12 ft or more.

When the exponent k is as small as it was found to be in this situation, it is convenient to represent the decreasing flow with increasing distance, (d), from the nest as a linear function over a small range of distance, with the slope proportional to the average rate of flow, and this gives

$$N_d = N_0(1 - 0{\cdot}00516d). \qquad (2)$$

Although a linear model of this kind implies, among other things, that the leakage process sets an ultimate limit to track length that is not acceptable (in this case the limit would be $1/0{\cdot}00516 = 194$ ft, a distance which is in practice often exceeded), the use of equation (2) gives what is for some purposes a useful prediction of flow-rates even at a distance of 70 ft (see Table 4, linear extrapolation). Certainly the numbers of ants leaving and rejoining per unit length of track, along any given short section of it, can be regarded as a constant fraction of the flow past some fixed point on that section, and this simplifies the interpretation of data relating to the steady density distribution taken up by foragers wandering freely over the inter-radial sectors, as will be seen later.

Relative densities of foragers were observed at twelve points arranged in three parallel lines $2\frac{1}{2}$ ft apart and running south-eastwards from, and at right angles to, the proximal section of track T 1, as shown in Fig. 1. The measurements were made by counting the number of ants seen, during a 10 s scrutiny, within a metal ring pressed on to the ground. Each point was sampled in turn—precautions having been taken to avoid undue disturbance of the vegetation—and the process repeated twenty times in quick succession.

The frequencies with which different numbers of ants were seen in the rings during two complete surveys made at different seasons are given in Table 6, and from them were calculated the mean relative densities, $\bar{n}$, and the variances, σ_n^2. These latter varied directly with the means, as would be expected; the distributions were adequately fitted by the Poisson series and could be normalized by using the $\sqrt{(n + 0{\cdot}38)}$ trans-

formation due to Anscombe (1948). The mean numbers are shown plotted against distance from the track in Fig. 3, from which it can be seen that in both experiments, but more obviously in the second, there was a decrease in abundance with increasing distance. Fig. 4 shows that the natural logarithms of the averages, n, obtained by grouping together all the lines, are to a first approximation a linear function of distance, and the weighted regressions are shown.

Table 6. *Surveys of inter-radial densities of foragers at site A*

Experiment, date, time and air temperature	Distance from track (ft)	Line	Number of ants (n) within ring Frequencies 0	1	2	3	4	Mean number ($\bar{n}$)	Variance of n
1.	2·5	1	8	8	3	1	—	0·85	
		2	9	7	3	1	—	0·80	
12 June		3	6	10	4	—	—	0·90	
		Sum	23	25	10	2	—	0·85	0·66
1500–1630 h G.M.T.	7·5	1	7	12	1	—	—	0·70	
		2	8	6	5	1	—	0·95	
9° C		3	11	6	2	1	—	0·65	
		Sum	26	24	8	2	—	0·77	0·71
	12·5	1	10	9	1	—	—	0·55	
		2	13	4	3	—	—	0·50	
		3	10	7	3	—	—	0·65	
		Sum	33	20	7	—	—	0·57	0·48
	17·5	1	13	5	1	—	1	0·55	
		2	12	5	3	—	—	0·55	
		3	9	7	3	1	—	0·80	
		Sum	34	17	7	1	1	0·63	0·77
2.	2·5	1	9	7	3	—	1	0·85	
		2	10	7	3	—	—	0·65	
29 August		3	10	6	3	1	—	0·75	
		Sum	29	20	9	1	1	0·75	0·79
1300–1445 h G.M.T.	7·5	1	15	4	1	—	—	0·30	
		2	11	8	1	—	—	0·50	
18° C		3	12	6	2	—	—	0·50	
		Sum	38	18	4	—	—	0·43	0·38
	12·5	1	14	6	—	—	—	0·30	
		2	15	5	—	—	—	0·25	
		3	14	4	2	—	—	0·40	
		Sum	43	15	2	—	—	0·32	0·28
	17·5	1	16	4	—	—	—	0·20	
		2	15	4	1	—	—	0·30	
		3	17	3	—	—	—	0·15	
		Sum	48	11	1	—	—	0·22	0·20

To make the experiments comparable the data were then reduced to the common units of apparent density per square foot, since a 9 in. diameter ring was used for the first experiment and a 6 in. one for the second; and finally all figures have been multiplied by the factor 1·111 to give estimates of the actual density. This latter operation was necessary since it was subsequently found, by supplementing a large number of 10 s scrutinies with prolonged searches under the vegetation within the rings, that on the average one in ten of the trapped ants had been passed unnoticed by the rapid method. When these adjustments had been made it was found that for

the first experiment the density of foragers, ${}_1L_d$, at a distance d from the track was given by

$$ {}_1L_d = 2{\cdot}243 \exp\{-0{\cdot}024d\}, \tag{3}$$

and for the second

$$ {}_2L_d = 5{\cdot}025 \exp\{-0{\cdot}083d\}. \tag{4}$$

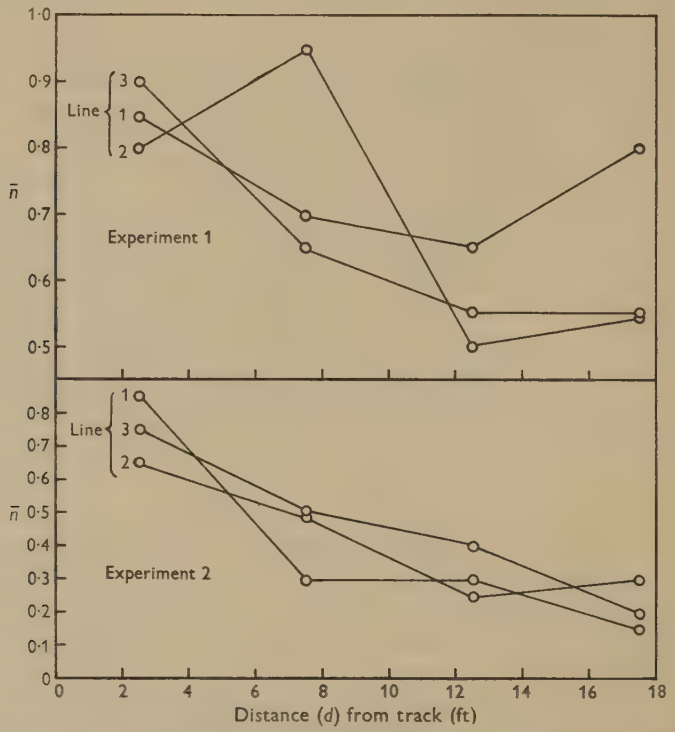

Fig. 3. Variation of density of foragers with distance from track T 1 at site A. Ordinates are the uncorrected averages of numbers of ants seen inside sampling rings (see text).

Exponential distributions of this kind are given by a simple mathematical model of the food-searching process, and this makes possible an interpretation of the constants of these equations. If it is supposed that when foragers leave the track they travel in straight lines at right angles to it, and that individual food units—whole organisms such as insects, or other solid particles—are distributed randomly over the area which is searched, then the probability, P, that food will not have been detected when a distance d has been traversed is

$$P = \exp\{-d/\bar{d}\},$$

where $\bar{d}$ is the mean distance. Now $\bar{d}$ will be inversely proportional to the number density, D, of the food units, and also approximately to their effective diameter, $2r$, provided this is small relative to the mean distance between particle centres. The effective diameter is determined by the average distance to which an ant has to

approach the prey before it establishes sensory contact and recognizes it as such. Then we may write

$$\bar{d} = 1/2rDs, \tag{5}$$

where s is a constant and is here a measure of the proportion of times that the prey is secured after contact has been made with it.

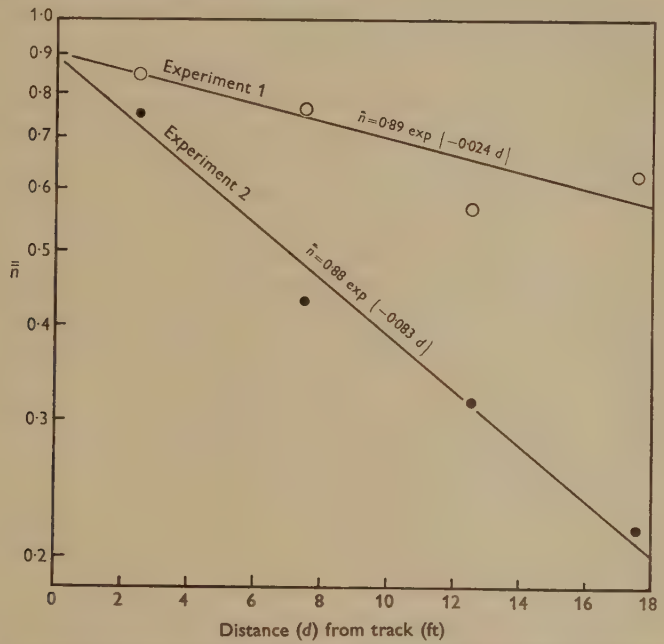

Fig. 4. Variation of natural logarithms of average forager density with distance from the track. Three sampling lines lumped together.

It can further be supposed that some time, y, elapses while the ant is more or less stationary and securing the prey before returning along the same route, and this interval is either constant or, if it is not, it will nevertheless be independent of the distance from the track that capture takes place. In any case observation suggests that that time is usually short compared with the time spent hunting.

If the leakage rate on one side from all points along a straight section of track is $I/2$ per foot per minute, then the density of outwardly moving foragers at a distance d from the track will be

$$I \exp\{-d/\bar{d}\}/2v,$$

where v is the average walking speed. When a steady state has been reached the same number of ants will be returning, and it has been found that the fact that they are burdened does not appreciably alter their speed. In addition, there will be a density of

$$Iy \exp\{-d/\bar{d}\}/2\bar{d}$$

ants in the act of securing prey, so that adding the three categories and substituting for $\bar{d}$ from equation (5) we have

$$L_d = I(yrDs + 1/v) \exp\{-2rDsd\}. \tag{6}$$

Although initially foragers move usually directly away from the track they appear to become progressively deviated from their course by obstacles, but nevertheless equation (6) might still be expected to be applicable, at least within reasonable distances of the track, provided that v is understood to be a resultant velocity, which also takes into account the possibility that the return route may be slightly different from the outward one, as it undoubtedly is in practice. The essential feature is that the search for food should be fairly highly oriented, leading the ant progressively away from the track without too much doubling back, and that the return journey should not be too different in direction. Without entering the discussion, summarized by MacGregor (1948), as to the means by which oriented movement is achieved in ants, it seems that this is roughly what happens in natural conditions where the foragers are most of the time out of direct sight of the rest.

Values of the product rDs, obtained directly by comparing equation (6) with equations (3) and (4) are 0·012 for the first experiment and 0·042 for the second. This implies that prey were three or four times as abundant in August as in June, provided that it can for the moment safely be assumed that r and s were unchanged. At both times small insects, chiefly Diptera, formed the bulk of the solid food brought back to the nest, and the fourfold difference is very roughly in agreement with subjective assessments made then of the abundance of flying insects. Observations of foragers catching midges (*Culicoides* species) and occasionally other small insects, which had settled particularly on the leaves of an ant-infested and easily accessible rowan, and also of their reaction to piles of artificial foods such as sugar, bread crumbs, and dead insects placed in their path, suggested that the perception radius r was of the order of 0·1 ft—not more—and that it did not vary greatly with the type of food. Of forty-three definite attacks on midges that I have observed, eighteen were successful; in the other cases either the ant turned away after apparently sighting the prey or it was unable to reach it before the insect flew off. It would probably not be far wrong to take the product rs to be rather less than 0·05 ft, thus giving absolute prey densities of about 1 ft^2 during the later experiment and 0·25 ft^2 during the earlier, which as far as can be judged are not unreasonable figures.

Rapid counts of the rate of flow past CP 1·3, made after the two density surveys described, gave the values 52 and 191 per min respectively (both directions; average of five 1 min batches). The corresponding rates measured rather more accurately just before the beginning of the surveys, in connexion with another experiment described later, were 46·4 and 215·9 per min. Taking the average rates during the surveys as 48 and 210 per min, approximately equivalent to values for N_0 of 50 and 217 per min, we obtain from equation (2):

$$_1I = 50 \times 0{\cdot}005\,162 = 0{\cdot}258/\text{ft/min}$$

and

$$_2I = 217 \times 0{\cdot}005\,162 = 1{\cdot}120/\text{ft/min}.$$

Since from equations (3), (4) and (6) the products $I(\sqrt{rDs} + 1/v)$ are 2·243 and 5·025, we have, for Exp. 1,

$$0{\cdot}012\,{}_1y + 1/{}_1v = 8{\cdot}69;$$

and for Exp. 2

$$0{\cdot}042\,{}_2y + 1/{}_2v = 4{\cdot}49.$$

The difference between these two figures is an indication of a difference in the pace at which hunting was conducted at the two times, and it is necessary to seek a reason for it. The analysis cannot be carried much further without an independent evaluation of the magnitudes of either the velocities v or the stationary intervals y. The latter must, however, have been relatively small because workers with prey trapped in the sampling ring were almost without exception actively walking back towards the nest. The time taken to secure a midge is rarely more than 1 min, and to accept a particle of artificial food less than half a minute, but this depends to a certain extent on the presence of other foragers at the pile, when acceptance is more rapid. Furthermore, v and the reciprocal of y might be expected to vary together as both are, in some degree, measures of the activity of the ants, so that the ratio $8{\cdot}69/4{\cdot}49 = 1{\cdot}93$ may be taken as an index of the relative rates of activity. The significance of this result is discussed in the next section.

At about the same time on the day following the second survey, an attempt was made to test the validity of the foraging hypothesis outlined above at another place in the same wood, site B. This was a smaller nest, about 4 ft in diameter, with a south-western exposure, situated at the foot of a rocky bank running to the north-west and south-east. The only track was a very wide one to a pine tree on the bank about 12 ft away from the mound centre and due north of it. Many of the workers, however, foraged in the open, nearly flat and rather boggy area to the south of the bank. The nearest trees on this side were a number of young birches 40 to 50 ft away and there was no other nest within 100 ft. The vegetation in the sector of radius 40 ft, lying between the directions 150 and 280°, was more or less homogeneous, and six lines of sampling points at intervals of 5 ft of radius were laid out in the directions 160°, 170°, 200°, 210°, 260° and 270°. Apparent densities were measured as before using the 9 in. ring.

The theoretical distribution applicable in this case, when the sector is fed from the perimeter track, instead of from a radial one as before, is

$$L_d = 2IR(yrDs + 1/v) \exp\{-2rDs(d-R)\}/d, \tag{7}$$

where R is the radius of the nest; d the distance from its centre; and I is now defined as the leakage rate per foot from the outer side of the perimeter track. The density thus declines rather more rapidly with increasing distance. The average numbers of foragers trapped within the sampling ring may be assumed to be proportional to L_d, and their logarithms will no longer be linearly related to the distance. Instead we have

$$\ln \bar{n}_d . d = A + Bd, \tag{8}$$

where A and B are constants.

Although there was a good deal of variation between the lines at site B, the averages for all lines of the numbers counted at each distance were fitted reasonably well by this equation, as is shown in Fig. 5, with $-B \equiv 2rDs$ approximately equal to 0·09, which is close to the value obtained the day before under similar weather conditions at site A. Variation was too great to allow a rigorous discrimination between equations (6) and (7) to be made, but plotting the logarithms of $\bar{n}_d$ directly against distance gave a much higher value, about 0·15, for the product $2rDs$. Although this could be explained in terms of a greater abundance of food at the second site it seems preferable

at the moment to accept equation (7) as giving the more satisfactory description of the distribution of foragers whose search originates at the nest instead of at points along a straight track. The hypothesis of constant leakage and random search as it has been defined here can, then, represent to a first approximation the foraging distributions observed under uniform weather conditions during the day, when it is expected that steady-states will be attained, irrespective of whether radial tracks are used or not: but it will be appreciated that the colonies used for these experiments were chosen because of the simplicity of the situations they presented for analysis, and it would be very much more difficult to interpret the distribution, say, between two curved paths running at an acute angle to each other.

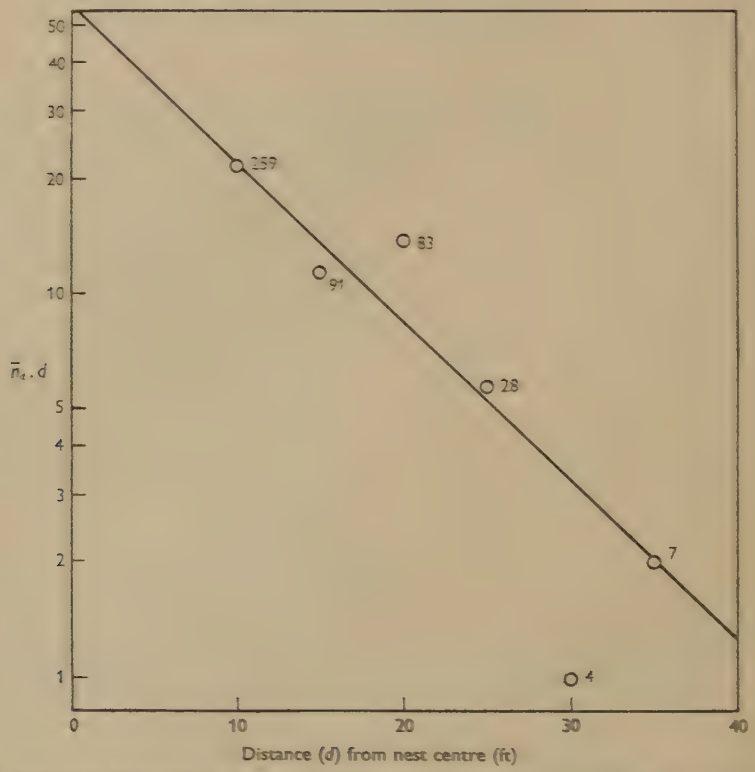

Fig. 5. Densities of foragers at site B. Ordinates are products of distance and the average number of ants seen inside sampling rings, and are plotted on a logarithmic scale. Figures by each point are total numbers seen in 120 samples taken at each distance (see text).

In the foregoing calculations it was assumed that the prey density was uniform over the searched area. If the ants were causing any considerable mortality by their predation, the prey populations, if they were more or less static, would become less abundant near the track or nest than away from it, though any such differential depletion would in turn mean that more foragers would pass through the proximal

zone and feed at a greater distance. In practice, however, the populations of food species are in constant flux, there being both movement on the ground and, in the majority of insects, intermittent flying; if this were not so Figs. 4 and 5 would show curvilinear trends. That the exchange rate between the trophoporic field and the air, or adjacent areas otherwise inaccessible to ants, is very high can be demonstrated by calculating the ratio of the overall rate of predatory depletion to the mean prey density (the 'standing crop'), in zones at various distances from the track. If the prey density remains more or less uniform in spite of predation this is given by $I(\phi^{d_1} - \phi^{d_2})\ 2D(d_2 - d_1)$ where d_1 and d_2 are the distances of the inner and outer boundaries of the zone, and $\phi = \exp\{-2rDs\}$, the term within brackets being the fraction of the foragers that find prey in that zone. The calculated rate of depletion in the 5 ft wide strip adjacent to the track was for example about 20% per hour during the first survey at site A and 60% per hour in the second. The corresponding figures for the band between 5 and 10 ft from the track are 15 and 40%/h, and for the prey densities to be maintained at the observed levels the rates of settling or invasion must be at least of this order, even when the replenishment of losses through normal movement out of the searched area is not taken into account.

It is of interest to consider briefly the possible use of equation (7) as a basis for developing more general models for the prediction of drift from wildlife reserves, in particular where a resident predator is feeding principally on nomadic species, since when the predators concerned are also nomadic another method, developed for studying fisheries problems concerning 'protected areas', would be a more appropriate starting-point. This is described elsewhere (Beverton & Holt, in press).

We suppose that in a highly idealized case the refuges of the predators are situated relatively close together in suitable country in the middle of a circular unfenced reservation, and that a balance is set up with the net reproductive rate of the prey just sufficient to support a steady population which continuously and rapidly redistributes itself over a wide but limited area so as to maintain a uniform density. The boundary of the reserve might be set somewhere within that area such that it contains at any given instant a certain high proportion of the total predators, but any sustained decline in the relative abundance of food will cause an overflow into the surrounding land which may be undesirable. If, for example, the boundary is set such that the index of drift (proportion of the predators outside the boundary at any time) is 0·1%, implying a ratio of reserve radius to mean free path of predators of $\ln 0{\cdot}001 = 6{\cdot}9$, then a decline of relative prey density, i.e. the ratio of number of prey to number of predators, by 10%—bringing $d/\bar{d}$ to 6·2—would double the drift. If the initial drift tolerance were higher, say 5%, the effect would be less critical, a drift rise of 35% being expected. It would be magnified, however, if the reduction in the standing crop of food organisms within the reserve was itself a result of increased predation. Thus suppose that with protection from human interference the predators doubled. Under some circumstances this might result in the prey density being reduced by nearly a half. With 5% initial tolerance, the drift would be expected to increase tenfold and might become a more serious problem. In practice of course natural heterogeneities of topography, vegetation and so on are likely partially to determine reserve boundaries, and invasion of the surrounds may be the result of a transient disturbance of the

space-time equilibrium—say by temporary overgrazing near the predators' refuges combined with slow recovery or redistribution of the prey—accompanied perhaps by qualitative changes in feeding habits; but although such factors would be in themselves of the greatest importance, they can with some justification be regarded as qualifications of the fundamental element in the foraging system, the average distance which the animal has to travel to obtain food. It should finally be mentioned that there is some evidence that this distance can also affect directly the mortality of a resident animal, because on it depends the amount of its time that the animal is outside its refuge and exposed to its enemies (Kalabukhov 1937).

THE EFFECT OF TEMPERATURE ON FORAGING ACTIVITY

Ribbands (1951) has demonstrated the importance of weather conditions in determining the flight range of the foraging honeybee. He found that in calm and warm weather the rate of gain in weight of his experimental colonies was usually higher than when it was cold and windy, and that this effect was increased when the bees were flying greater distances to the crops. It was concluded by Brian & Brian (1951) that high insolation of ant habitats 'improved conditions directly by raising temperature, and indirectly by stimulating herb growth, and so producing a proximate (and probably better) food supply'. These authors showed that in *Myrmica rubra* L., small colony size may be associated with low temperature and food deficiency. They argued that the latter may be more apparent than real if temperature affects the activity of workers and hence their ability to capture agile prey organisms; but in woodlands, where in fact ants have to travel relatively further for their supply of plant juices than when they are living in the open, the prolongation of already long journey times would be perhaps the most important result of a temperature decrease.

Pickles (1935) found that the activity of all the species of ants which he studied is highest in hot sultry weather and lowest when cold and windy, though in woodland wind variation is less than in the open and does not play such an important part. In particular the ground temperature rather than the air temperature is important. The effect of temperature on the rates of vital processes is the subject of a voluminous literature, and the connecting laws that have been proposed were recently reviewed by Allee, Emerson, Park, Park & Schmidt (1949), who concluded that the general relationship might be a sigmoid one, holding until an upper temperature limit is approached, where disintegrative processes become dominant. Data relating to the middle region of such a curve will be adequately graduated by the linear function favoured, for example, by Shelford (1930) and Chapman (1931). At lower temperatures it is common to find that the relationships are exponential (Thompson 1942), although when attempts are made to increase the range of temperature over which 'van't Hoff's rule' is applied it is usually found necessary to vary the temperature coefficient itself. Fry (1947), in discussing temperature as a controlling factor of animal activity, remarked that the use of the exponential coefficient as an indicator of differences between species had the disadvantage that it measures only slope and not position on the temperature scale. However, the fact that relative changes in velocity with temperature can thereby be defined by a single parameter instead of the

two required by a linear expression may itself be a great advantage when the effects of, say, normal seasonal or diurnal fluctuations of temperature on the movements of a population are being considered.

Most of the experiments with wood ants here described were made at temperatures (θ) between 8 and 22° C, and, at least over that range, the effect of temperature on the rate of locomotion of poikilothermic animals is satisfactorily represented by the equation $Q_{10} = v_{\theta+10}/v_\theta = 2{\cdot}0$ to $3{\cdot}0$ approximately in many cases that have been studied (e.g. Fry (1947)—goldfish; Pantin (1924)—marine amoebae; Crozier (1924)—millepedes; my own data for *Paramecium* (unpubl.), and others). Shapley (1924) measured the average time taken by ten or twenty individuals of a number of species of trail-running Dolichoderine ants to run a distance of 30 cm at various temperatures and observed a general agreement in their behaviour. He found, for example, that for *Liometopum apiculatum* Mayr at temperatures below 20° C, Q_{10} was about 3·3—a high value. He also found that ants carrying burdens of food continued to run normally at temperatures slightly above those at which unburdened ones behaved erratically, but does not mention any differences of behaviour at lower temperatures.

Further evidence that ants react in a simple way to temperature changes within the above-mentioned range is provided by Deal's (1941) experiments on the so-called temperature preferendum of *Acanthomyops* sp. He found that these ants—and also some other insects—when placed in a temperature gradient, instead of accumulating at an 'optimum' distributed themselves in such a way that when a steady state had been reached they were most abundant at the cool end of the apparatus (8° C), and progressively fewer were found at increasing temperatures up to 30° C. This, apart from some distortion at the end of the apparatus, is in general what would be expected to happen in a closed space within which movement was random but the velocity increased continuously with temperature, just as the U-shaped distribution of some of his other experimental species would be expected if the maximum of the velocity/temperature curve (the 'optimum' activity temperature) happened to occur near the middle of the temperature range in the apparatus.

Data relating to the track walking speeds of *F. rufa* are summarized in Table 7. The times taken to run between two threads 6 in. apart stretched at right angles across the track at site B (halfway between the nest and the infested pine) at CP 1·1–1·2, site A, were measured. Personal bias in selection of the ants to be timed was avoided by observing each time the *n*th one to cross the thread after an arbitrarily chosen instant, *n* being a random digit between three and six inclusive.

Parry (1951) has shown that metabolism and evaporation probably do not affect the body temperatures of terrestrial Arthropods in sunlight. Although he found that the air temperature near the ground changes very rapidly between the surface and 1 in. above it, in my experiments both the actual temperatures and the differences between the measurements in 'free air' (2 ft above the ground) and at $\frac{1}{4}$ in. from the surface were much less than in his. It is probable that my measurements, consistently made at the latter distance using a mercury thermometer with a blackened bulb, reflected fairly well the variations in body temperature of the ants. This could not of course necessarily be assumed if comparisons were to be made between, say, night and day temperatures and activities, when radiation conditions are greatly different

(Wellington 1950), but my observations were on the whole made in the middle of the day during clear weather.

No significant differences between uphill and downhill speeds were found, nor any effect of burden. Reciprocals of the times taken to run the measured distance in each sample were on the whole more nearly symmetrically distributed than the times themselves, with a tendency to positive skewness at the higher temperatures due

Table 7. *Variation of walking speed with temperature. Tyndrum, sites A and B*

Site and reference number	Number in sample	Temperature (°C)			Average speed, $\bar{v}$ ft/min	S.D. v
		Before	After	Average		
A1*	9	8·5	8·0	8·25	1·21	0·29
2*	30	8·5	9·0	8·75	1·28	0·30
3*	26	8·5	8·5	8·5	1·30	0·39
4	20	10·0	10·0	10·0	1·23	0·28
5	20	10·0	10·0	10·0	1·39	0·26
6*	18	11·5	12·0	11·75	1·53	0·59
7*	20	12·5	12·0	12·25	1·48	0·38
8	20	12·5	12·5	12·5	1·62	0·38
9	20	14·0	12·5	13·25	1·91	0·52
10	19	15·5	15·5	15·5	2·48	0·49
11*	20	16·5	17·5	17·0	3·20	0·61
12	20	18·5	19·0	18·75	2·76	0·50
13*	37	20·0	20·0	20·0	2·88	0·57
14*	28	20·0	20·5	20·25	2·78	0·41
15*	40	21·0	21·0	21·0	2·81	0·63
16*	40	21·5	20·0	20·75	2·66	0·73
17*	40	20·5	21·0	20·75	3·05	0·57
B1	48	9·0	9·0	9·0	1·16	0·35
2	20	9·5	10·0	9·75	1·18	0·25
3	20	10·5	10·5	10·5	1·29	0·44
4	20	10·5	11·5	11·0	1·28	0·32
5	40	12·5	12·0	12·25	1·65	0·39
6	21	12·5	12·5	12·5	1·48	0·48
7	22	13·5	13·5	13·5	1·72	0·76
8	20	15·0	14·0	14·5	1·80	0·60
9	20	14·5	14·5	14·5	1·59	0·51
10	20	16·0	16·0	16·0	2·31	0·74
11	20	17·0	17·5	17·25	2·08	0·79
12	20	17·5	17·5	17·5	2·23	0·57
13	17	18·0	17·0	17·5	2·52	0·56

* All site A data at CP 1·1–1·2 unless otherwise stated:
A 1. Positive direction only.
A 2 and 3. At same time as series 6 (Table 3) and first density survey. A 3 at CP 1·4–1·5.
A 6 and 7. At same time. A 7 measured at CP 1·3.
A 11. Track blocked at CP 1·5 (see p. 26).
A 13 and 14. At same time as series 3 (Table 3) and second density survey. A 14 at CP 1·4–1·5.
A 15–17. All within 1 h. For A 16 and 17 track was brushed clear of debris. A 16 at CP 1·3 (see p. 26).

presumably to the approach to a universal 'optimum'. Variation of walking speeds, arising through both the existence of differences between individuals and wandering within the measured distance, increased with speed and temperature up to about 18° C and then slightly decreased. The logarithms of the mean velocities at site A are plotted against temperature in Fig. 6, and considering that these data were obtained in the field throughout a season and not under controlled conditions the relationship up to

18° C is well enough represented by a straight line, giving a constant $Q_{10}=2{\cdot}5$. These results are in accord with Shapley's (1924) finding that speed can be quite accurately predicted from temperature alone, without bringing in other environmental factors such as humidity.

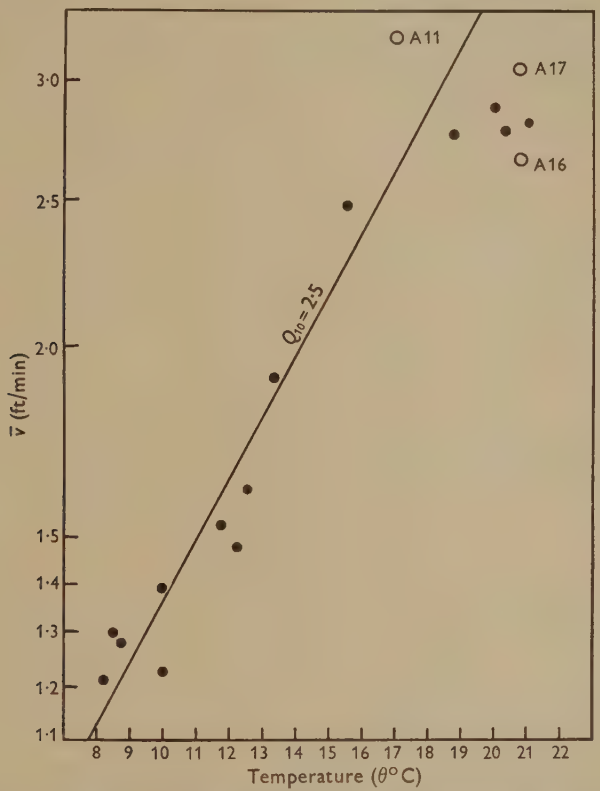

Fig. 6. Variation of walking speed with temperature at site A. Ordinates plotted on logarithmic scale. For significance of points with sample number marked see notes to Table 7.

Walking speeds on this open section of track were higher than the average speeds over the whole length of T 1 at similar temperatures. Thus crumbs of cake thrown on the track near CP 1·6 were beginning to be carried back past CP 1·3, 64 ft away, after 36 min, and laden ants were passing in numbers 42 min after the first outwardly going forager reaching the pile accepted the food, giving an average speed of about 1·5 ft/min at 18–20° C. Rates of progress would be even slower through the vegetation away from tracks, and the minimum net values of v for the two density surveys, obtained by putting $y=0$ in equation (6), viz. $1/8{\cdot}69=0{\cdot}12$ ft/min and $1/4{\cdot}49=0{\cdot}22$ ft/min respectively, seem to be quite reasonable. The temperature difference between the two surveys is alone sufficient to account for the difference between these speeds; the value of Q_{10} for the foraging process given by them, on the assumption that temperature is the only significant factor, is 2·1—that is, near to the usual quoted values. Therefore,

if other factors were operating, they were probably either not very important, or in this case cancelled each other.

If both the total number of foragers and the average distance travelled on each sortie remained constant, increased running speed at higher temperatures would be expected to result in a proportionately greater flow along the tracks. Referring back to Table 3 it will be seen that there is indeed a positive correlation between flow and temperature, but that the temperature coefficient is very high, Q_{10} being about 5. In general the high temperatures refer to times when insects were abundant and therefore foragers were finding prey relatively close to the nest, but without further information it is not possible to say how much the high temperature index is due to this, or to there being a greater number of foragers active in the warmer weather. For series 6 and 3, which correspond with the two density surveys, some of the required information is available if the analysis of the last section is accepted, since the average distances from the track at which prey were being found can be computed: they are $\bar{d} = 1/2rDs = 40$ and 12 ft for surveys 1 and 2 respectively. In the first case it is calculated that about seventy times as long a period was on the average spent searching for food as in walking down the mean track distance of 6 ft, twenty-five times as long in the second. Assuming, therefore, that the average circuit speeds changed roughly in the same proportion as the speeds of progression in the undergrowth we may calculate the ratio of flow rates that would have been expected if the two surveys had taken place under the same temperature conditions, viz.

$$\frac{{}_2I_1v}{{}_1I_2v} = \frac{1{\cdot}120 \times 4{\cdot}49}{0{\cdot}258 \times 8{\cdot}69} = 2{\cdot}2.$$

This is not very different from the distance ratio $(40-6)/(12-6) = 2{\cdot}56$, which suggests that the number of ants foraging had not changed much. In fact, however, this section of track and its adjacent area cannot legitimately be considered in isolation, as particular ants do not always use the same track, or depart from it, at the same distance from the nest. It seems unlikely that the average journey distance for the whole colony changed by as much as the ratio 2·56 since most foragers spent a greater proportion of their time on the tracks, tree trunks and branches. Further, a number of factors determine the activity of workers in the nest, and although temperature must be one of them, this tends to be maintained at a high but steady level by the heat-absorbing and insulating properties of the dome and the opening and closing of entrances (Steiner, 1930). The time spent in the nest by a forager between sorties would therefore probably not be affected by fluctuations in air temperature so much as the journey times, if at all. The possibility that rather more foragers were active during the August experiment than during the earlier one cannot therefore be entirely ruled out.

Gilmour, Waterhouse & McIntyre (1946) give data, summarized here in Table 8, on the dispersal of blowflies, *Lucilia cuprina* Wied., that illustrate the effect of temperature on the movements of a nomadic species, and enable a comparison to be made with the resident ants. By inspection of the results of four experiments, in each of which a batch of marked flies was released at a point and the positions of subsequent recaptures plotted, they concluded that of the three environmental conditions

measured, temperature was the most important single factor affecting activity, although the rate of dispersal did not vary directly with it, and high humidity and strong winds may have had depressive effects. It was found that apart from small discrepancies, caused either by the catch per trap not being a completely reliable index of population density or by the existence of considerable differences between the activities of individual flies, the distribution in space and its changes in time were consistent with the 'random walk' hypothesis. The logarithms of density were linearly related to the ratio d^2/kt, where t was the time elapsed between release and

Table 8. *Dispersal of marked blowflies*

(From Gilmour, Waterhouse & McIntyre 1946.)

Exp.	Dispersal index (miles)	k'	Mean temperature (° C)	Mean relative humidity (%)	Average wind speed, (w miles h)
1	2·15	4·62	21·1	41	4·6
2	0·43	0·18	17·2	63	8·7
3	1·70	2·89	24·9	27	7·2
4	1·40	1·96	18·7	25	6·2

capture. d the distance travelled, and k the velocity coefficient of diffusion, which should be proportional to the speed of movement of the organisms if the mean free path remains constant. The dispersal index given by these authors is 'the radius of a circle beyond which half of the released flies had passed at the end of the second day of trapping', i.e. about 2½ days after release, and its square provides a relative measure (k') of k for each experiment. During the third and fourth experiments the average wind speeds and relative humidities were nearly the same, but there was a six degree temperature difference and a direct estimate can thus be obtained of Q_{10}, namely 1·9.

A remarkable feature of these experiments is that in spite of the prevailing wind, dispersion was symmetrical and the centre of density remained stationary. There was a fair amount of day-to-day variation in the recorded wind flow, and these observations suggest that the weather was rather gusty and that the insects only flew when the wind dropped to a velocity such that it did not appreciably hinder flight in any direction. That many flying insects behave like this is common experience: Allee *et al.* (1949) point out that wind in an exposed habitat is a special handicap to animals with weak powers of flight and that various devices are employed to overcome it, including darting rapidly from shelter to shelter. If this view is correct, wind effects could be eliminated by dividing the values of k' by estimates of the proportion of time spent actually flying, q, which, in the absence of detailed information about the frequency distribution of wind velocity, might to a first approximation be regarded as a linear function of the average wind speed, w, viz.

$$q = 1 - cw,$$

where c is a constant. This simple expression has the required limiting characteristics that when $w = 0$, $q = 1$ and as w increases towards a certain high value, q decreases to zero. It can be derived by assuming that the mean velocities when the wind was

below a threshold speed, and when it was above it, remained constant, and that only the relative frequency and duration of low and high winds changed. The threshold is considered to be constant over the relatively small temperature range observed. If the wind never dropped below the threshold the anemometer readings would be higher than $w = 1/c$, and no dispersal would be expected.

With the assumption of linearity we may write

$$k' = k'_0(1 - cw) \exp\{(\theta - \theta_0)V\},$$

where V is the exponential temperature coefficient and k'_0 the square of the theoretical dispersal index at some arbitrary temperature θ_0 in dead calm weather. If any value of V between 0·10 and 0·14 (corresponding with Q_{10} from 2·7 to 4·0) is taken, the

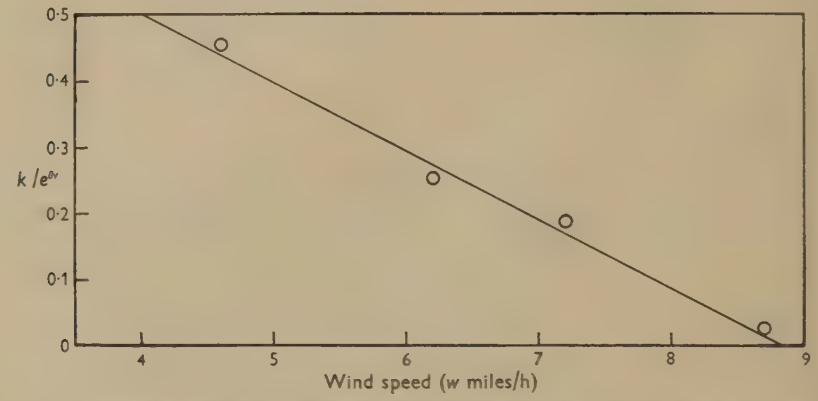

Fig. 7. Relation between wind speed and temperature-corrected dispersal rates of marked blowflies. Data from Gilmour *et al.* (1946).

relationship between $k' \exp\{-(\theta - \theta_0)V\}$ and w is reasonably well represented by a straight line. A good fit to the points for the first, second and third experiments, which does not at the same time imply a negative value of $k' \exp\{-(\theta - \theta_0)V\}$ for the fourth is obtained when $V = 0{\cdot}11$ ($Q = 3$), giving $k'_0 = 0{\cdot}9$ and $c = 0{\cdot}11$. This is illustrated in Fig. 7, where θ_0 has been taken as zero. The signs and magnitudes of the deviations are not obviously related in any simple and consistent way to the prevailing humidities. The predicted maximum wind speed in which *Lucilia* will fly, given by the intersect of the straight line of Fig. 7 with the x-axis, is about 9 miles h. This is not apparently inconsistent with Thompson's (1942) statement that a common flying speed for most insects is 4–9 miles h, but that the larger Diptera are rather faster. Larger insects would be expected to fly in stronger winds. Park (1928) found that honeybees will generally not forage when the wind velocity exceeds 15 miles h and this is also the average speed at which a laden bee returns to the hive in dead calm conditions

If 9 miles h can be taken as the actual flying speed at 20° C, the average temperature at which the blowfly experiments were conducted, an estimate of the free-flying path can be obtained using the 'random walk' model. The dispersal index at this tempera-

ture in calm weather would be about 2·8. From tables of the area of the normal curve we find that this is 0·67 of the standard deviation of recapture distance, which latter is therefore $2{\cdot}8\ 0{\cdot}67 = 4{\cdot}2$. The flies were active only during the hours 8 a.m.–5 p.m., i.e. about 22 h during each of the $2\frac{1}{2}$-day experiments. This gives a value of k, the diffusion coefficient, of $4{\cdot}2^2\ 22 = 0{\cdot}8$, and since k is $8\ \pi^2$ times the product of speed and mean free path, a value for the latter is just under a ninth of a mile. Although this result has no particular intrinsic interest, the calculation has been carried through to demonstrate the possibility of using data from surveys of animal density changes to calculate parameters that would be expected to be directly related to the causes of interruption in movement. In the present case a proportional relationship between the ratio speed mean free path, i.e. the number of random movements per unit time (about 80 per hour), and the abundance of sheep in the area, might be sought.

The foregoing analysis has shown that the blowfly data, so far as they go, lend support to the hypothesis that the gross effects of temperature on dispersal may under normal conditions be predicted roughly by varying the velocity parameter of the appropriate distribution function according to van't Hoff's rule. Burla, da Cunha, Cavalcanti, Dobzhansky & Pavan (1950) give their own and Dobzhansky and Wright's figures for the dispersal of mutant *Drosophila*, and in both cases the logarithms of the standard deviations of recapture distance (given in metres per day) are approximately linearly related to the temperatures during the experiments, giving $Q_{10} = 3{\cdot}0$ to $3{\cdot}2$ over the range 15 to 25° C.

To summarize: with resident species searching an unlimited area the journey times, and hence the flow-rate and the amount of food brought back to the refuge, may be affected by temperature, but the steady-state density distribution of foragers remains unchanged; the steady distribution attained by nomadic animals moving freely within a limited area would likewise be unaffected by temperature, but if they are spreading from a centre over an unlimited area (or in the early stages of dispersal within a limited one) the transient densities depend on the temperature up till that time, as do the numbers of contacts with food particles. The order of magnitude of this effect may be illustrated by reference to the dispersal of young fish from the nursery grounds mentioned in the introduction. Although the data have not been analysed with this question in mind, the median distance from the coast of a brood at any given age would be expected to vary as the square root of k. Taking $Q_{10} = 3$ this means that a change of 1° C in the average temperature, a frequent occurrence according to Tait (1952), would alter this distance by 6%; a change of 4° C, such as may happen in an exceptionally cold winter, would alter it by 25%, so that climatic variations could have a practical significance out of proportion to their apparent magnitude.

It should finally be mentioned that the effect of temperature on food gathering by resident species may be obscured where foraging time is controlled to a large extent by other variables, particularly in, say, flying insects where the journey itself may occupy a relatively small fraction of the duration of the round trip. Thus Brian (1952) could detect no effect of temperature on the foraging activity of *Bombus agrorum* Fabricius, though the amount of rainfall was important.

THE EFFECTS OF OBSTRUCTIONS ON THE TRACK

Although no systematic survey was attempted of the effects on foraging activity of seasonal changes in the amount of accumulated litter which partially blocked the main paths, the data given in Table 7 indicate that such hindrances were not entirely negligible. The walking speed given for sample A 15 was measured when the track was strewn with debris, mainly small twigs and pine needles, as it normally was through much of the year. When these were swept away, and the speed was measured immediately afterwards, a rise of nearly 10% was recorded (A 17) though the temperature was the same, and it is probable that the effects of seasonal changes in the vegetation between the tracks would be at least as much as this. In addition, foragers may obstruct each other, especially when the rate of flow is very high, but the results would only be noticeable where the ground conditions limit the width of the track. This is so, for example, on parts of T 1 at site A, where it passes frequently between rocks set close together. It was noticed whilst batch A 12 was being recorded that head-on 'collisions' between ants going in opposite directions appeared to be an important cause of delay, especially as they were frequently followed by a mutual examination with the antennae. The rate of flow negatively was 12 l/min at that time, and immediately afterwards a pile of earth was placed over the track at CP 1·5 thus temporarily interrupting the returning workers. When the positive flow at CP 1·1–1·2 was reduced almost to nothing, the average walking speed increased from 2·76 to 3·20 ft/min (A 11). Differences in track width can have a similar effect, for example when the walking speed between CP 1·1 and 1·2 (width about 6 in.) was 3·05 ft/min (A 17) it only averaged 2·66 ft/min over the short section just past CP 1·3 where all the foragers ran between two rocks only 2 in. apart (A 16).

If it is assumed that the frequency with which an ant encounters those moving in opposition to it is proportional to the opposing rate of flow per unit width of track and that each collision results in a delay of fixed duration ϕ, then the walking speed (v) would be given by

$$v = v'(1 - KN\phi/u);$$

where v' is the theoretical speed when there is no opposition, N is the rate of flow, u the width of the track and K is a constant. A linear relationship between speed and flow arising from a rather different cause was found by Smeed & Bennett (1949) for motor vehicles in London streets. An obvious implication of it is that an increase in the number of ants or vehicles using a particular path will result in a decrease in the number of journeys completed by each in a day. If congestion occurs all along the track then it may readily be shown that the average journey time is linearly related to the reciprocal of the number of foragers, so that the total number of journeys, and hence the food intake, increases towards an asymptote as the number of foragers increases. This is therefore one of the minor ways in which competition between the members of a colony (competition in the sense that the foraging success of one individual depends inversely on that of the others) may limit its size.

THE NUMBER OF FORAGERS AND THEIR INTAKE OF FOOD

Neither of the two methods commonly used for estimating the size of animal populations by recapture of marked individuals is applicable to these ant colonies. In the capture–recapture method (Lincoln Index) reviewed by Bailey (1951), it is assumed either that mixing of marked and unmarked animals is complete or that all samples are taken absolutely at random, and it is difficult to see how in this case the experiment could be arranged so that either of these conditions obtained. The other method requires that the sampling process itself should be an important cause of mortality, so that it can be used normally only for census of commercially exploited populations such as fish or game (Ricker 1948, Beverton & Holt, in press). Another approach to the enumeration of resident populations is possible however, and it incidentally avoids the difficulty of finding a type of mark that ants cannot remove from each other, since for this method the proportion of individuals that lose their tags during the experiment is probably unimportant so long as it is not excessive.

We suppose that N animals continuously make foraging circuits all of which pass through a common point, for example in the present case the junction of a radial track with the perimeter. These circuits are of various lengths and take different times to complete. The ants can be classified at any instant according to the time they require to carry out the whole of their current trip. In a steady state this distribution of trip times will not be expected to change in the mass even if the trip times taken by an individual do vary in repeated journeys.

Let $f(t)\mathrm{d}t$ be the proportion of ants for which the current trip time lies in the elementary interval $t \pm \frac{1}{2}\mathrm{d}t$, so that

$$\int_0^\infty f(t)\mathrm{d}t = 1.$$

Of those on a journey of duration t, the fraction 1 t will on the average be completing their trips every unit interval of time, for by reason of the assumed steady state the ants of each class may be taken as uniformly distributed with regard to the instant they will complete their present trip. The expected total number completing their journey every unit of time, which is the rate of flow past the common point, will be

$$I = N\int_0^\infty f(t)\,\frac{1}{t}\,\mathrm{d}t.$$

Now the harmonic mean, T, of the current journey times for all ants (each reckoned once only) is defined by

$$\frac{1}{T} = \int_0^\infty f(t)\,\frac{1}{t}\,\mathrm{d}t.$$

Hence $N = IT$.

The measurement of I is straightforward, and if T can be determined this immediately gives an estimate of N. Now any particular trip time t can be resolved into two parts: $t = t_1 + t_2$, where t_1 is the time to pass from the outside of the nest and back to it after foraging, and t_2 is the time spent inside the nest before starting out again. Both of these parts might be estimated by marking ants so that particular individuals can be recognized as they pass, and repass in the opposite direction, an observation

point close to the nest. If, however, the ants to be marked are chosen in a manner similar to that described for the speed tests there is clearly a sampling bias in favour of those travelling at higher speeds or for shorter distances. The amount of bias is in fact proportional to the reciprocal of the trip time, so that the arithmetic mean, $\bar{t}$, of the observed times that elapse between marking outgoing ants and observing them passing the census point on the return journey estimates T. Such an estimate would have to be corrected by adding to it the delay in the nest between journeys, to give the time taken for a full circuit.

I am indebted to Mr J. G. Skellam for the following derivation of the equation relating numbers, trip-time and rate of flow in the general case. Let the individual ants be classified according to their mean journey time, μ, and let the proportion of them having mean journey time in the elementary interval $\mu \pm \frac{1}{2}\mathrm{d}\mu$ be $g(\mu)\mathrm{d}\mu$. Each ant then makes, in unit time, an average of $1/\mu$ appearances at a comprehensive observation point. In a sample marked as they leave the nest the proportion of individuals having mean journey time $\mu \pm \frac{1}{2}\mathrm{d}\mu$ is

$$h(\mu)\mathrm{d}\mu = \frac{\frac{1}{\mu}.g(\mu)\mathrm{d}\mu}{\int \frac{1}{\mu}.g(\mu)\mathrm{d}\mu}.$$

The mean observed journey time for this sample is then

$$\bar{t} = \int \mu h(\mu)\mathrm{d}\mu = \frac{\int g(\mu)\mathrm{d}\mu}{\int \frac{1}{\mu} g(\mu)\mathrm{d}\mu} = \frac{\text{number of ants}}{\text{rate of flow to or from the nest}}.$$

For our purpose it is therefore only necessary to be able to identify members of a particular group of ants, and batches of outgoing foragers were marked with coloured cellulose paint as they left the nest, without lifting them from the track. With practice it proved possible to do this without greatly disturbing them. The results of a census made at site A at midday (air temperature 14–16° C) during July are given in Table 9. The total rate of flow was measured by counting five 1 min batches alternately at each of five census points, which were chosen on each of the five main radiating tracks to be as near to the nest as was possible and convenient. Previous counts showed that track 3 consistently carried more traffic than track 1, and track 5 carried less. Tracks 2 and 4 were of about the same capacity as track 1. These findings are reflected in the data quoted, which also show that at the time there were no important differences in the flow in opposite directions, and it may be assumed that the foraging distribution had effectively attained a steady state. Again, it was not possible for this experiment to mark on and watch more than a single path, but trial experiments showed that T 1 was fairly typical. On T 3, the longest track and the one with most forkings, the average time taken was never more than twice as long as on T 1: T 5 was short and the journeys short; tracks 1, 2 and 4 were about equal.

Of fifty foragers marked as they left the nest by T 1, just before the measurements of the rate of flow were started, forty-two were seen to pass CP 1·1 at the end of their return journey within 3 hr. No more had returned after another hour and it was presumed that the remaining eight had been overlooked or had returned by another route. The mean time taken by those that were seen again was 129 min. The distribution of journey times was nearly symmetrical, with a standard deviation of 22 min (Table 10), so that the standard error is rather less than 3% of the mean. The minimum figure for the number of foragers is then $370 \times 129 \simeq 48000$.

Table 9. *Rates of flow during marking experiments at site A*

Census point ...	1·1		2		3		4		5	
Direction ...	+	−	+	−	+	−	+	−	+	−
Ants/min	71	64	86	50	96	110	68	64	50	73
	80	72	87	80	102	73	73	69	49	48
	69	74	86	62	88	91	67	67	62	53
	69	72	84	84	95	92	80	66	58	51
	73	78	80	83	100	84	64	82	57	62
Means	72·4	72·0	84·6	71·8	96·2	90·0	70·4	69·6	55·2	57·4
	72·2		78·2		93·1		70·0		56·3	

Total+ 378·8 Total− 360·8 Average 369·8 (370)

The average time spent by foragers inside the nest between journeys was estimated under similar weather conditions at site C in another wood (Pass of Leny, Perthshire, Nelmes 1938), which was found after most of the work described at Tyndrum had been completed, and offered an ideal situation for track running and marking experiments. Here a large nest had been built against the south side of a stone wall, along the top of which ran the only two tracks used by the colony, one eastwards, the other westwards, and each terminating at groups of pines 30 or 40 yd away. Fifty returning ants, which were presumed to be carrying loads of honeydew, were marked with

Table 10. *Journey times of 42 marked foragers on T 1, site A*

Time (min)...	60–70	70–80	80–90	90–100	100–110	110–120
Number	1	0	0	1	6	3
Time (min)...	120–130	130–140	140–150	150–160	160–170	170–180
Number	9	10	4	5	1	2

yellow paint just before they entered the nest from the east, and at the same time fifty were marked green as they entered from the west. The tracks were watched by two observers for 2 h and the numbers seen again leaving the nest are recorded in Table 11, together with the average time since marking. The experiment was repeated later the same day using different colours.

It is evident that a particular forager does not always use the same track. Nevertheless, there appears to be a slight tendency to emerge on the same track that the previous trip had been made on, although it may be that in the long run an ant will use all tracks equally. The average time of 31 min obtained in these experiments is perhaps an underestimate since some slow-moving individuals might have been missed by the

restriction of watching time to 2 h. Also, although the effect of marking on the subsequent activity of the ants is not known, it seems more likely to have delayed than hastened their unloading. Applying then this figure to the Tyndrum data a revised estimate of the active forager population of colony A is obtained thus:

$$370 \times (129 + 31) \simeq 59000.$$

Table 11. *Marking experiment at Callander, site C, to estimate the time spent inside the nest between journeys*

		Marked			
		East		West	
Expt.		Number	Average time (min)	Number	Average time (min)
1	Seen East	16	39	14	32
	Seen West	16	48	23	35
2	Seen East	26	24	27	33
	Seen West	20	21	29	24

This estimate of total flow does not include those few ants which left the perimeter track by routes other than the radials, to forage directly in the inter-radial sectors. These were at most 5% of the total, and it is probably safe to say that the number of ants actively collecting food for this colony in July was of the order of 70000. This is consistent with the figures for total worker population in this species given by other investigators who have dug up nests and made direct counts. Although it is said that the size of the mound is not necessarily a sure indication of the number of inhabitants, colony A was, judging by the territory occupied by it, a relatively large one, and for large wood-ant nests total worker populations of up to 100000 or even 150000 have been quoted (Donisthorpe 1927, Elton 1932).

Table 12. *Positive flow throughout the day at CP1·1, site A*

Time (G.M.T.) ...	0655–0705	0755–0805	0855–0905	0955–1005	1055–1105	1155–1205	1255–1305
Temperature (° C)	11·0	11·0	12·5	12·0	13·0	14·0	14·5
Flow per min	52·3	60·1	65·7	68·0	74·5	74·1	72·0
Time (G.M.T.) ...	1355–1405	1455–1505	1555–1605	1655–1705	1755–1805	1855–1905	1955–2005
Temperature (° C)	16·0	15·5	15·0	15·5	14·0	12·5	12·0
Flow per min	79·4	82·2	81·6	76·6	77·9	69·4	71·3

The rates of flow in a positive direction past CP 1·1 (site A) throughout the day on which the marking experiments were made are given in Table 12. Each value is the mean of ten 1 min batches counted between 5 min before and 5 min after the hour, and it will be seen that they tend to follow the air temperature changes, which latter were measured to the nearest 0·5° C. The total number of journeys completed in the 14 h between 6·30 a.m. and 8·30 p.m. is estimated to have been about 600000, and as track 1 carried about one-fifth of the colony's traffic the total for the nest was 3000000. Of all the returning foragers counted 19% were recorded as carrying solid food in

their jaws. In this connexion it is worth noting that Donisthorpe estimated the catch of insects by a large colony as nearly 100000 daily.

The average weight of a load of honeydew was found to be about 0·0019 g by taking the difference between the weights of samples of foragers ascending the pine tree and of those descending. These are given in Table 13. The weights of three samples of 100 ants taken as they passed CP 1·1 carrying burdens of solid food (insects, spiders, etc.) were 1·84, 1·52 and 2·01 g, so that the average weight of a solid load was about 0·008 g. These samples included occasional larger prey being carried by two or more workers. The total intake of food to the colony during the part of the day observed was

$$300000\ (0{\cdot}19 \times 0{\cdot}008 + 0{\cdot}81 \times 0{\cdot}0015) = 820\ \text{g},$$

of which 44% was honeydew and the remainder solids. The biomass of foragers was $70000 \times 0{\cdot}0098 \simeq 700$ g, and although they continued work at night, activity was at a very low level, so that each was probably bringing in on the average one and a half

Table 13. *Weights of foragers sampled at site A as they passed CP 1·6*

(Weight (g) of ten samples, each of 100 foragers.)

Direction						Mean/100
−	1·01	0·98	0·97	0·98	0·96	0·0098
+	1·16	1·15	1·16	1·17	1·21	0·0117
						Difference −0·0019

times its own weight of food during the whole day. It is interesting to note that White (1871), who counted the number (204) of ants passing in one direction in 5 min along a *Formica rufa* track, calculated that the daily traffic to and from the nest, along its five 'roads' 1–6 in. in breadth and up to 76 paces long, totalled 600000 (i.e. 300000 journeys at the low rate of flow of 40 min), but this was assuming that not only were the ants working throughout the 24 h of that summer day, but their activity was undiminished at night, which is unlikely to have been true.

The above data make an interesting comparison with those quoted by Butler (1949) referring to the honeybee, an insect weighing nine or ten times as much as the wood ant. The latter carries either its own weight of solids or one-fifth of its weight of honeydew; a bee's load is about two-thirds of her weight of honey, half of water or less than one-third of pollen. However, the number of trips made per day by a bee varies greatly, from about fifty for water-collecting to seven with pollen, so that although she may bring back during a day rather less than her own weight of pollen, twenty-five times that amount of water would not be unusual. When it is remembered how much the values given for both species depend on the particular conditions prevailing during the experiments, it appears that their economies as far as foraging efficiency is concerned are not very different.

In a study of the relationships between wood ants and the rest of the fauna and the flora of a forest, the number of active foragers in a colony may be in some ways a more useful index of its size and influence than the total number of individuals, and it is certainly easier to estimate without taking the drastic action of digging up the nest. Although it will often be impracticable to take censuses on all tracks used, both

year to year and seasonal changes in the size and activity of a colony, and simultaneously the food intake, could be assessed by observation of representative parts of the foraging system. Determination of the rate of exchange of some prey species in and out of the ants' trophoporic field, so that some evaluation might be available of the mortality due to predation, has been attempted by watching the settling frequency of biting-midges on the leaves of a rowan favoured by them, in different weather conditions. This has raised other problems, the two most important of which should briefly be mentioned. It is true that most of the ants that climb trees bring back aphid excreta, but not all. When counts were made of workers descending from the rowan it was found that not only did the proportion that brought back midges depend on the number of midges settled at the time, but that when the latter were abundant relatively more ants explored this tree than the nearby pine to which another fork of the same trail ran, so that there was an intensification of foraging in the region of high prey density. Related to this observation is the second problem, that of variation of the perception radius. Elton has described the aggregation of wood ants at a broken twig from which sap was oozing, and Wheeler (1926) pointed out that ants rapidly congregate where one of them f[illegible] so that a form of communication must exist. It is not, however, n[illegible]y a complex process such as occurs in the honeybee. Perhaps the simplest form of information exchange between animals searching for food occurs when one sees another feeding. When a small heap of artificial food is placed on an ant path, passing unladen workers are more likely to stop and feed at it if one or more others are already there, until the accumulation of ants reaches a maximum, and only declines as the size of the pile itself diminishes. The extent to which social predation at this level does in practice increase the total intake of food, which depends as much on the degree of aggregation of the food organisms as on the methods of communication and response involved, is a matter for future investigation.

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SUMMARY

1. The number of foraging workers in a wood ant colony is given by the product of the harmonic mean duration of all round trips made and the number of trips completed per unit time. These two quantities may be estimated by marking and census methods, to facilitate which a simple recording apparatus for use in the field has been developed, and the results obtained are consistent with counts of total population of ant mounds that have been quoted in the literature.

2. A simple mathematical model fits satisfactorily the data available on the distribution of foragers over the trophoporic field of the colony, and prediction of the effects of changes in density of the prey populations has been attempted. The effects of temperature, and also of obstruction to free movement, on the rate at which food is gathered

are considered. Distinction is made between the dispersal of nomadic animals and of resident ones which, like ants, return periodically to a home base; some implications of the type of distribution pattern found, as they bear on the determination of the optimum size of a certain type of wildlife reserve, are briefly discussed.

NOTE

Since I wrote the above account, my attention has been drawn to a paper by A. H. Duncan-Weatherley (1953), and some correspondences between our observations should be noted. Rate of flow measurements for the Australian ants were made along radiating trails and across observation lines laid down in the sectors between. It was found that most foragers used the trails and that the numbers active decreased with distance from the nest, although for most of the day the rates of flow in each direction, at any one point, were about equal. Rates of flow ('activity'), increased in the first part of the day and decreased in the second, but there was usually also a temporary decrease during the hottest part of the day when the temperature was about 26° C.

Duncan-Weatherley also noted the apparent lack of co-ordination between individuals working to carry large pieces of material for or from the nest, and this observation may be rather important in the construction of further theoretical models of foraging populations.

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THE DYNAMICS OF THE ZONATION OF THE COMMON PERIWINKLE (*LITTORINA LITTOREA* (L.)) ON A STONY BEACH

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(With 7 Figures in the Text)

INTRODUCTION

The common periwinkle, *Littorina littorea* (L.), is found where conditions are favourable around the entire British coastline except perhaps in the Isles of Scilly. It was not recorded from the isles by Browne & Vallentin (1904) and one of us (J. E. S.) failed to find it on the shores of St Mary's and St Agnes in 1951. It is rare or absent on shifting substrata of shingle and unconsolidated sand, does not appear to favour rocks of chalk and limestone or shores exposed to the full force of storm waves (Evans 1947), and is most abundant on sheltered stony or rocky beaches. Periwinkles are often taken in the dredge below tide marks (Huntsman 1918, Wright 1936, Mistakidis 1951), and it is probable that some individuals are permanently submerged throughout life. *L. littorea* is, nevertheless, characteristically intertidal in habit.

The first accurate survey of the distribution and vertical intertidal range of *L. littorea* was made by Colman (1933) on the moderately sheltered shore at Wembury, South Devon. The periwinkle is here virtually confined to the zone normally subject to diurnal submergence and exposure by the passage of the tides—the 'middle shore' of Yonge (1949). Evans (1947), in confirming Colman's findings for the Wembury traverses, showed, in addition, that the vertical range may be displaced a little to the seaward on more sheltered beaches or towards the land where there is a greater degree of exposure to storm waves.

The selection of the middle shore by *L. littorea* as its most favoured habitat shows that while it can tolerate a fairly wide range of temperature, salinity and exposure to air, site selection is in some way linked with a need or preference for conditions of alternating cover and exposure. This is most evident when the conditions are limiting, as at the landward side of a shore animal's range. The shore littorinids *L. neritoides*, *L. rudis* and *L. littorea*, for example, each have their own sharply defined upper limit of distribution (Colman 1933, Evans 1947, and others) in conformity, doubtless, with their different capacities for sustained activity in the absence of periodic seawater cover (Colgan 1910). The more gradual falling off in numbers and the successive disappearance of the three species at the seaward side of their range is not, however, so readily explicable. It is not thought that prolongation of the period of immersion is limiting since all three species can withstand immersion for several days, even *L. neritoides*, which lives on rocks above the reach of most tides, sometimes living in pools under permanent cover of water (Lysaght 1941). It is therefore evident that while the landward extension of an intertidally living marine animal is linked directly

with its toleration of semi-aerial conditions the numerical distribution of a mobile animal such as *L. littorea* within its normal territory of the middle shore is controlled not so much by the limiting conditions of its existence as by requirements of a less urgent kind, such as perhaps the nature and quantity of food available. But it is this second feature of zonation, namely a recognizable pattern of distribution within an animal's normal range, which is the more direct manifestation of individual and group behaviour, for while as this paper will show in the instance of *L. littorea* very few animals ever get the opportunity of testing out their behavioural responses against the more rigorous conditions of life at the top of the middle shore, most of them have an extensive territory lower down the beach available for exploration. The patterns of distribution that emerge in consequence of the selection of territory by each of the great number of individuals within a shore population constitutes the dynamic aspect of zonation.

A study of the dynamics of zonation, though not bearing directly on the nature of the behavioural mechanisms concerned in the selection by the periwinkle of suitable ecological sites, can, if the necessary precautions are taken, provide information of value in the subsequent analysis of these mechanisms. In tracing the nature and extent of the displacements and redistributions of the middle shore populations at different times of the year particular care has therefore been taken to distinguish between locomotory displacements and those brought about by external circumstances such as wave action. A brief consideration of the events leading to a zoned distribution of the periwinkle will serve to indicate the scope and aims of the present survey and the problems under review. Three principal phases can be distinguished in the creation of a vertically zoned population, all of which are, as will be shown, continuously in operation.

During the phase of offshore dispersal of the eggs, embryos and larvae, and until the post-larval winkles are able to evade planktonic life by crawling or holding on to the substratum, the distribution of the brood is primarily determined not by any behaviour on their own part but by the movements of the water in which they are suspended. The main questions at issue at this stage are the nature and direction of the dispersal, and whether the young post-larval animals are deposited at the close of planktonic life, in the main, intertidally or on the sea bottom below low-water mark.

The sorting process which leads to zonation occurs during the phase of re-population of the shore. Except in the unlikely possibility that all the young brood are from the first deposited directly on the beach, and in a pattern exactly corresponding to the distribution of the adult population, some sorting must occur. The change from the post-larval to the adult distribution may in theory entail a differential mortality of the brood at the different shore levels, which if of itself effective, would imply no significant movement, behavioural or otherwise, subsequent to settlement. The zonation of sessile animals such as barnacles is brought about in this way. Alternatively, there may be a redistribution of the population of young periwinkles either as a result of wave sorting or of locomotory movements, with the possibility in either event that the change from the juvenile to the adult distribution may take place either on the beach itself or involve the shoreward progression of the metamorphosed brood, after settlement, from the offshore plankton along the sea floor and open beach.

The vertical zonation of *L. littorea* as commonly understood involves the maintenance of the adult pattern of zonation. Since the individual animals of the zoned population rarely stay in one position for long, the questions here arising concern the nature of the movements and their relation to the maintenance of a distributional equilibrium.

THE SITE OF THE SURVEY

The site and bearing of the transect upon which the survey was based are shown in Fig. 1. The shoreline off the town of Whitstable here runs in a roughly north-easterly–south-westerly direction, the transect at right-angles to the shore having a bearing of 315° (magnetic).

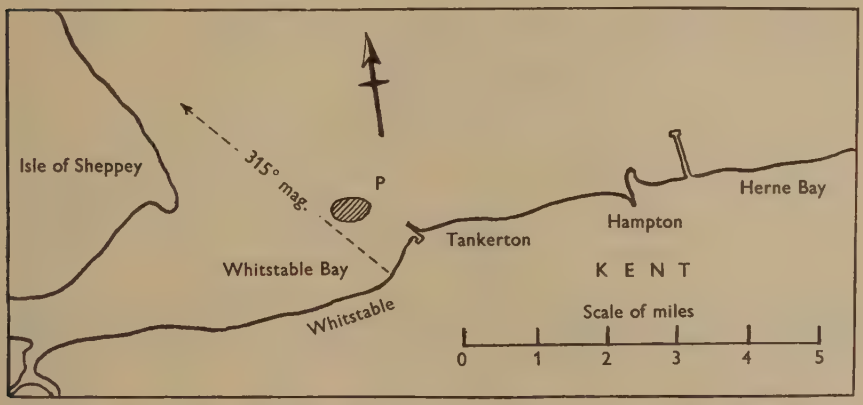

Fig. 1. Sketch map of a part of the Kent coast showing the position and bearing of the beach transect from which collections of *L. littorea* were made and the area (P) where plankton samples were taken.

At low water of spring tides the sea retreats almost half a mile from high-water mark. Fig. 2, a section through the transect, illustrates in detail only the upper part of the beach from the level of mean high-water spring tides (M.H.W.S.) to a little below the mean tide level (M.T.L.). At the shoreward end of the transect the beach shelves rapidly (1 in 9) as a bank of loose shingle, devoid of periwinkles. Near the level of mean high-water neap tides there is an abrupt change in the gradient and physical character of the beach. The downward slope, following a 1 in 45 declination for about 300 ft, is studded with stones firmly bound in a muddy sand which overlies the bed of London Clay to some depth. Observations have shown that these stones are not moved about even by rough seas (Newell, in press). Though dry in places, most of the stony beach is beset with puddles of standing water connected here and there by drainage runnels. Stations 1–6, on which the survey was primarily based, spanned this part of the beach where periwinkles were always plentiful. Each station was marked by a low cairn of stones as were the five stations (7–11) on the almost level 'flats' stretching seaward from the lower margin of the stony beach. The flats, except at their seaward margin, are covered with fine sand mixed with silt (Chapman 1949), and are without surface stones or other binding material. No littorinids were ever found on this part

of the muddy flats (stations 7 and 8). Nearer low-water mark the fine sand thins out and is replaced by shell debris (stations 9 and 10). At the lowest levels of exposure the stiff underlying London Clay is laid bare (station 11). Some periwinkles were almost always found at stations 9–11, though never in the same number as at stations 1–6. It was not, therefore, found necessary, on every occasion, to collect from the lower stations.

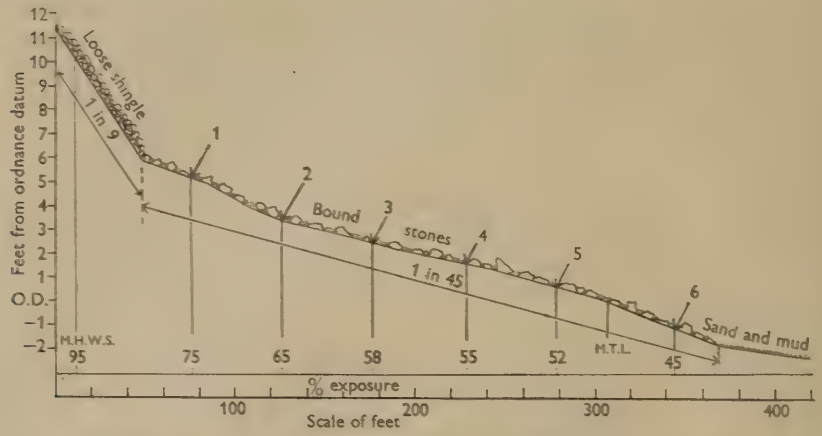

Fig. 2. A diagrammatic section of the transect showing the positions and levels of stations 1–6. To the right of the figure sand and mud flats continue to E.L.W.S. at a slope of 1 in 200 for about 75 ft and then of 1 in 600 for about 1900 ft. Stations were at the following distances from M.H.W.S.: 7—600 ft, 8—800 ft, 9—1650 ft, 10—2000 ft, 11—2100 ft.

COLLECTION AND TREATMENT OF THE SAMPLES

The samples were taken by hand-picking all the periwinkles (*L. littorea* and *L. rudis*) found within a previously marked off area of one square metre, the animals lying on the tops of stones being removed first. A careful examination was then made of the undersurfaces of the stones and of the underlying sand and mud for further specimens. The collections were stored in tins and, except in two instances when they were preserved in formalin, examined fresh and then preserved for later reference.

This method of collecting almost certainly results in some animals being overlooked. From the point of view of the present survey the two most serious consequences of these deficiencies are likely to be an underestimation of the number and proportion of the first-year animals on the shore, and the probability that the very smallest animals, at the time of their invasion of the shore, remain undiscovered. It has, however, been possible to keep a check on these points by comparing the size distribution of the *L. rudis* and *L. littorea* populations from identical sites.

In sorting the samples a separation was first made of the two species. With the larger animals this could be done rapidly and accurately on their distinctive shell characters. Some of the smaller specimens were, however, less readily distinguishable and, in the first four collections, before this was fully realized, some of the younger *L. littorea* were found on later examination of the preserved shells to have been

wrongly assigned to *L. rudis*. In subsequent samples, therefore, all animals with a shell less than 6 mm long were examined for tentacle markings as well as shell shape, and the survey was continued beyond the period originally planned in order to duplicate the October and November collections. In all, twenty collections were made from October 1951 to November 1952, at intervals of approximately three weeks at alternating times of spring and neap tides. The number of animals in the samples varied from about 300 to 1200 and averaged about 600 (Table 1). The shells of all the animals were measured to the nearest millimetre along the axis of the columella from the shell apex to the lowermost edge of the inner lip bordering the aperture. The size distribution of animals from the stations 1–6 in the different collections is set out in Table 2.

Table 1. *Numbers of* Littorina littorea *taken from square metre areas*

	Station number						
	1	2	3	4	5	6	Total
1951							
7 Oct.	1	14	246	95	120	117	593
21 Oct.	27	184	154	68	46	67	546
17 Nov.	10	187	86	48	38	64	433
9 Dec.	1	21	75	72	128	18	315
30 Dec.	0	29	80	121	72	112	414
1952							
22 Jan.	0	39	101	81	21	42	284
10 Feb.	0	43	146	69	95	119	472
24 Feb.	0	47	176	98	106	161	588
17 Mar.	0	40	128	99	105	99	471
8 Apr.	0	70	210	126	84	126	616
30 Apr.	5	143	278	118	72	126	742
18 May	2	78	211	107	24	85	507
3 June	0	245	655	97	64	154	1215
24 June	0	73	127	68	43	98	409
16 July	0	310	266	105	175	112	968
9 Aug.	0	332	209	242	123	145	1051
29 Aug.	0	198	459	147	65	102	971
19 Sept.	2	144	166	83	47	79	521
3 Oct.	0	71	227	171	18	74	561
7 Nov.	1	55	108	101	58	100	423
Total	49	2323	4108	2116	1504	2000	12100

After measurement, the shell of every *Littorina* was examined for encrusting barnacles and an estimate made of the extent of coverage. The ways in which the barnacle coverage of animals more than one year old can be used in defining the position of periwinkles on the shore at the end of the emergent phase of zonation, and in tracing their subsequent movements, are discussed later in their appropriate context.

It will be found convenient during the course of this paper to refer from time to time to the age-groups of the periwinkles found on the Whitstable beach. The approximate size-range of the various groups are: first year, shell length 2–12 mm; second year, 13–16 mm; third year and older animals, 17 mm and over. These size-ranges have been determined by tracing the progression of the modal numbers of

animals from the time of the main egg emission (data in Table 2) and by noting the size at which an encrustation of barnacles first occurs. This happens when the animals are about 12 months old.

Table 2. Littorina littorea: *Distribution of size-groups in successive collections, 7 October 1951 to 11 November 1952*

Shell length (mm groups)																			
<5	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	>21	Total
—	1	—	3	6	14	32	54	55	57	119	123	63	39	15	8	4	1	—	594
—	—	—	1	—	11	30	64	61	64	85	118	43	37	18	12	1	1	—	546
—	1	—	—	3	8	20	39	46	42	82	82	38	23	26	5	11	—	1	433
—	—	4	1	6	25	37	35	20	30	43	51	27	14	15	5	2	—	—	315
—	—	1	3	5	26	77	81	32	27	44	62	25	14	11	3	3	—	—	414
—	1	6	1	4	16	23	33	35	33	32	55	23	13	2	3	—	1	—	281
—	5	6	2	6	23	60	67	50	50	63	171	30	18	10	5	4	2	—	472
3	5	6	5	6	17	52	81	52	59	100	124	35	21	13	5	3	1	—	588
—	6	9	10	8	19	49	60	54	38	53	40	49	28	19	10	16	3	—	471
—	—	9	21	14	14	35	60	60	55	75	66	93	52	35	8	12	3	4	616
—	5	2	29	45	21	50	93	133	83	127	78	33	26	16	1	—	—	—	742
1	1	10	25	34	27	18	48	105	79	75	55	14	6	4	4	1	—	—	507
1	3	6	14	38	35	28	50	172	254	246	210	76	48	21	5	8	—	—	1215
2	3	2	14	15	12	20	18	54	82	80	68	22	14	2	2	—	—	—	410
—	2	3	4	23	37	38	42	119	199	171	119	55	24	14	3	1	2	—	856
3	4	5	10	25	56	62	67	160	233	192	131	57	29	10	7	—	—	—	1051
3	3	12	15	9	29	59	52	126	196	167	160	71	40	21	7	—	1	—	971
10	4	3	6	7	16	25	28	64	125	107	76	35	16	1	3	—	—	—	526
9	2	2	9	7	21	33	45	115	101	106	56	33	12	9	1	—	—	—	561
14	18	12	7	14	17	32	23	63	64	52	46	26	20	11	3	1	—	—	423

SAMPLING AND POPULATION STATISTICS

The population statistics needed for the study of the dynamics of the vertical zonation of *L. littorea* are the absolute number of animals and the proportion of the various age-groups present at the different beach horizons at different times. Patchiness in the distribution of the population as a whole, in consequence of the tendency of *L. littorea* to aggregate in wet places and to avoid dry ones, precludes the possibility of making an accurate tally from small-scale samples of the absolute number of animals present at the different beach levels at any one time. The general distributional pattern is best judged from features that persist over long periods of time when the effects of patchiness are evened out by the taking of samples from both wet and dry stations. The limitations which an unevenly distributed population imposes on the tracing of possible mass movements are, moreover, less serious than might at first sight be expected on account of the information concerning the movements of periwinkles which is independently provided by the study of the displacements of barnacle-marked shells.

An accurate estimate of the proportion of the various age-groups in the populations at the different shore horizons is especially important in the tracing of the distribution of the young brood during the emergence of zonation. It is therefore necessary to know the extent to which small samples reflect the general pattern of distribution of the post-larval juveniles on the shore and their subsequent sorting into populations having particular zonal characteristics at the different levels of the beach. The

adequacy of the sampling with this end in view can be judged from Table 3. The percentage proportions of the first-year, second-year and older animals in the twenty collections made over stations 1–6 of the transect are shown in the left-hand section of the table. Except in the first three instances where the number of the first-year animals was underestimated owing to the faulty identification of the youngest stages (p. 38), there is a general similarity in the population structure in the series of collections which is seen, on excluding the first-year animals, to be based on a virtual constancy of proportion of the second year and of the older animals (Table 3, middle section). If now the proportions of the first- and second-year groups (right-hand

Table 3. *Percentage proportion of 1-year, 2-year, and older* Littorina littorea *from collections taken from stations 1–6*

Date of collection	1-yr	2-yr	> 2-yr	2-yr	> 2-yr	1-yr	2-yr	
1951								
7 Oct.	28	60	12	84	16	31	69	
21 Oct.	30	57	13	82	18	35	65	
17 Nov.	28	58	14	80	20	33	67	
9 Dec.	40	48	12	81	19	46	54	
30 Dec.	54	39	7	84	16	59	41	
1952								
22 Jan.	42	51	7	88	12	45	55	
10 Feb.	46	46	8	84	16	50	50	
24 Feb.	39	54	7	88	12	42	58	
17 Mar.	45	38	17	70	30	55	45	
8 Apr.	35	47	18	72	28	43	57	
30 Apr.	51	43	6	89	11	54	46	
18 May	52	45	3	94	6	54	46	*a*
3 June	28	64	7	90	10	31	69	*a*
24 June	34	62	4	93	7	36	65	
16 July	32	63	5	92	8	33	67	
9 Aug.	37	58	5	92	8	39	61	
29 Aug.	32	61	7	90	10	34	66	
19 Sept.	31	65	4	94	6	32	68	*b*
3 Oct.	44	53	4	93	7	45	55	*b*
7 Nov.	47	45	8	84	16	52	48	

section) are considered it will be seen that while the proportions fluctuate more rapidly and extensively from one collection to another there are two major discontinuities in the series indicated in the table at *a* and *b*. The first (*a*) is marked by a fall and the second (*b*) by a rise in the number of first-year periwinkles relative to the second-year group. Both are sustained long enough to show that they reflect real conditions and are not due to errors of sampling. The first break occurs, in fact, at the time of the main spawning period when a great number of periwinkles of the previous year's brood are passing into their second year; the second discontinuity marks the first appearance, in any great number, of the new brood on the beach. There appears to be no doubt then that, on the whole, the sampling methods faithfully record the population structure and that the method is sensitive to the real changes in the constitution of the population which it was hoped to record.

THE OFFSHORE DISPERSAL OF EGGS AND LARVAE AND THE AVAILABILITY OF NEW BROOD

The encapsulated fertilized eggs of *L. littorea* are spawned at the time of tide cover and are carried offshore with the ebbing tide. Capsules are found in the inshore plankton off Plymouth at all times of the year though they are most abundant in February and March (Lebour 1937, 1947). At Øresund, in Danish waters, on the other hand, Thorson (1946) has found the greatest concentration of early stages during June, July and August, none being present in February and March. Further records of the main spawning period are March–May, Heligoland (Linke 1933); March–September, Brittany (Caullery & Pelseneer 1910); January–June, Ireland (Tattersall 1920); January–July, Millport (Elmhirst 1923) and April–July, St Andrews, Bay of Fundy (Hayes 1929). It would seem, therefore, that *L. littorea* is potentially capable of breeding all the year round with a maximum ovulation at a time when the rising spring or early summer temperatures reach a critical level, but that the winter temperatures in the different regions named may fall, for a longer or a shorter period, below the minimum required for spawning.

At Whitstable, in 1952, the first considerable emission of encapsulated eggs took place on 25 or 26 April, for on the latter date the inshore plankton contained great numbers of uncleaved eggs. On 30 April the embryos were still within the capsule but by 25 May they had passed through the veliger stage and had metamorphosed into shelled juveniles with a shell about 0·25 mm long. Mixed with the tiny periwinkles and in about equal numbers were embryos in an early stage of segmentation. This accords with the rhythmic spawning to which Thorson (1946) refers, and is here linked to the spring tides of the new moon (24 April and 23 May).

Plankton samples taken in July, August, September and October all contained a few larvae as well as juvenile periwinkles, but neither eggs nor larvae were noticed in the few plankton hauls made during the winter of 1951–52. However, the presence of young (5 mm) *L. littorea* on the shore in April, May and June 1952 strongly suggested that eggs had been present in the plankton during some of the winter months. This view has been confirmed by the as yet unpublished work of A. M. El Maghraby who has taken regular three-weekly plankton hauls throughout 1953 in an area about 1 mile (Fig. 1, P) offshore from the site of the shore survey. Maghraby found that the eggs of *L. littorea* were present throughout the whole of the winter. They were scarce in January but became common in February and abundant in April and May.

The newly metamorphosed *L. littorea* with 0·25 mm. high shells are, at the age of one month, equipped for crawling and can, it may be presumed, adopt a bottom-living habit if given opportunity. They may, however, continue to grow during an extended period of pelagic life (Thorson, 1946). It is not known how long the planktonic phase normally lasts in the Whitstable waters. The shallowness of the water for a considerable distance beyond low-water mark, and the suitability of the substratum for settlement suggests, however, that pelagic life is not unduly protracted, a view which is confirmed by the fact that none of the post-larvae taken in the Whitstable plankton has been found to have a shell as much as 0·5 mm long. It may

therefore be concluded that juvenile periwinkles are available for the repopulation of the shore over the greater part of the year, and perhaps in warmer winters over the whole year, with a maximum settlement in April, May and June; that the youngest of the crawling stages are of about 0·25–0·5 mm shell height; and that their place of settlement is either on the shore itself or on the sea bottom seaward of low-water mark.

REPOPULATION OF THE SHORE AND EMERGENCE OF ZONATION

However carefully hand-collecting is done some periwinkles will be overlooked, and the samples are likely to be most deficient in their representation of the smallest animals. An estimate of the probable misrepresentation was sought by comparing on three occasions the numbers of *L. rudis* in hand-picked and sieved samples from adjacent square-metre areas, *L. rudis* being chosen for this purpose because of its smaller size and the known occurrence at all times of the year of the youngest stages. The comparison showed that while few animals more than 5 mm long were missed by hand-collecting, there may be as much as a tenfold increase in the number of the smaller shells after sieving. A similar deficiency must therefore be suspected in the number of the younger *L. littorea* with the additional possibility that the very smallest periwinkles may be entirely overlooked and their first appearance on the beach pass unnoticed.

Of the 12000 or so *L. littorea* collected over the period of a year the smallest had a shell 2·5 mm long; only two were of this size. There were 12 of 3 mm; 34 of 4 mm; 64 of 5 mm; 98 of 6 mm; 180 of 7 mm; 275 of 8 mm; 444 of 9 mm; and 780 of 10 mm. More than 1000 of each of the 11–15 mm groups were taken, the numbers in the larger size-groups declining progressively, only five animals of 22 mm or larger being found (Table 2). A most striking feature of this distribution is the very low proportion of the smaller shells, a mere 48 out of 12000 animals (0·4%) being less than 5 mm long. On the assumption, based on the *L. rudis* figures, that there were in reality ten times that number present, the proportion is still only of the order of 4% of the whole population. On the eight occasions when comparable counts were made of the *L. rudis* size distribution, of the 3334 animals measured 560, or 17% of the population, were 4 mm or smaller. With the appropriate adjustments made for sampling deficiencies, the beach population of *L. rudis* would contain more than 60% of animals less than 5 mm long, a figure ample for the replenishment of an adult population wholly recruited from brood spawned directly on to the beach and never plankton-borne. How then is the *L. littorea* size-distribution to be interpreted? The proportion of the animals of a size-range identical with that of the smaller *L. rudis* is 0·4% or on adjustment 4%, a concentration wholly inadequate for the maintenance of adult stocks. It must therefore be concluded that there is a continual recruitment of the population by the migration on to the beach of young periwinkles from the sublittoral sea floor and the lower reaches of the beach. The question then arises, at what stage in the life of the periwinkle does the inshore movement begin? Do they reach the shore at the immediate post-metamorphic stage or do they move in after a period of growth on the sea bottom below low-water mark? The answer to this question depends upon the significance that can be placed on the fact that only

two animals 2·5 mm long, and none smaller, were found on the beach. Since more than 400 *L. rudis* smaller than 2·5 mm have been taken in only eight unsieved, hand-picked collections this must surely mean, in spite of the most cautious reservations attendant upon the method of sampling, that the absence from the collections of the youngest *L. littorea* is of real significance, and that they are in fact either absent or exceedingly rare on the Whitstable beach.

There are a number of references in the literature to the occurrence on the shore of *L. littorea* brood, but it does not appear that the size of the smallest animals on their first appearance on the beach has ever been explicitly stated. Moore (1937), however, speaks of finding young periwinkles on the Trevol flats of the River Tamar at the beginning of July, and his graph (fig. 1, p. 724) of the growth-rate shows the young to be 2·5 mm long, the same size as the smallest Whitstable specimens. It will be recalled (p. 42) that the largest of the juvenile winkles taken in the plankton had a shell length of 0·5 mm at the most. With the smallest animals on the shore 2·5 mm long it is difficult to escape the conclusion that during the intervening period they have been living offshore on the sea floor from whence they are either cast upon the beach by wave action or undertake an active shoreward migration. There is evidence, in the area surveyed, that both passive and active movements occur, and that their relative importance in the repopulating of a shore depends primarily on the physical nature of the beach substratum.

The stony beach from which most of the collections were made is approached from the sea, at low water, by more than 600 yd of almost level flats, in the muddy sand of which are few stones or other objects where periwinkles can attach and find shelter. The periwinkles occasionally to be found here, when the tide is out, are in constant movement over the wet surface. Even on the calmest of days, when ripples barely an inch high lap gently on the beach, the larger periwinkles caught by the advancing tide while on the exposed flats, and without the means of a foothold, are tumbled over by tiny waves as they break on the shore and are rolled forward in the swash. On the almost level flat the backwash is much less powerful than the forward surge and displaced objects are not, as a rule, swept back to their original position. The total resultant shoreward shift, on a calm day, is not more than a few feet for, with the rapid advance of the tide over the flat, the periwinkles quickly become covered by water sufficient in depth to prevent an effective forward thrust being felt on the bottom. No observations were made of the effect of larger waves nor of the extent of the movement of the smallest periwinkles which are difficult to keep in view in broken water. So far as could be judged, however, from the movements of small stones, objects not so large as to resist displacement by the forwardly moving swash, and yet not small enough to be incorporated in the interstices of the particles of mud and sand, are liable to be carried shorewards over the flat. It can be assumed, in view of previous considerations that young periwinkles, on leaving the plankton, are not less than 0·5 mm in shell diameter. At this size they are considerably bigger than the largest of the sand grains on the flat which were found to be not more than 0·1 mm in diameter. Little periwinkles, being larger and less dense than the sand grains, would thus, on settling from the plankton, tend to remain on the surface of the substratum, and any of them reaching the flats would almost inevitably be rolled by wave action up the

shore at least as far as the lower margin of the more steeply shelving beach of bound stones upon which the main survey was based.

The stony beach, unlike the flats, presents many obstacles to the further transport of periwinkles by wave action. The stones form hummocks separated by intersecting crevices and depressions in which small animals find lodgement and shelter from the waves. Even after heavy storms there was, on general inspection, no obvious change in the general distribution of the periwinkles on this part of the beach. There is indeed, in the instance of the larger animals, direct evidence of the inability of breaking waves to cause more than local displacements of periwinkles on the stony beach. Of greater relevance to present considerations, however, is the observation based on careful analysis of the collections, that the *L. rudis* populations, with a size range of 1·5–12 mm shell length, show no significant change of vertical distribution, either in respect to total number of animals present, or in the proportion of the different age-groups over the period of a year. This size-range of *L. rudis* happens to correspond almost exactly with that of the first-year *L. littorea* and is a strong indication that any movements and changes in the zonational distribution of the first-year animals are not to be attributed to wave sorting but are the result of self-determined movements the course and extent of which will now be considered.

The histograms in Fig. 3 show the way in which the first-year animals are distributed over the transect stations 1–6 of the stony beach. The total number of animals in particular size-groups (A–D) within the first-year range (< 5, 5 and 6 mm; 7 and 8 mm; 9 and 10 mm; 11 and 12 mm) taken from the six stations during the year was recorded, and the proportion occurring at each station plotted as a percentage (black columns). It will be noted on comparing the series of unshaded columns (winter collections, October 1951–April 1952) with the obliquely hatched series (summer collections, April–November 1952) that there is an almost identical distribution, in the two periods, of all the size-groups. The relatively small number of animals taken on each occasion of collecting made it impossible to check the distribution over shorter periods of time effectively, but there was never any clear indication of a distribution differing at any particular period or occasion from that which characterizes the year's collections as a whole. It is, therefore, justifiable to measure the extent and direction of the changing distribution during the first year of life by reference to the year-over occurrence of the successive growth stages.

It will be seen from Fig. 3 and Table 4 that the youngest animals (Fig. 3A) are most numerous over the lower stations (4–6) of the transect, and that with increasing age (B–D) there is a gradual shoreward shift of distribution which is expressed in the four graphs of Fig. 3 by the progression to the left of the centre of distribution, the position of which is marked by an arrow. This upward displacement of the population of young periwinkles during their first year of life on the shore may be real or apparent according to whether it is brought about by an actual upshore movement or by differential juvenile mortality on the different beach horizons, the changing distribution requiring in this instance a higher death-rate on the lower than on the upper levels. There is, in fact, no indication either from the presence in greater number of dead shells, or in the more rapid decline in the numbers of living animals, that the death-rate among young *L. littorea* is substantially greater on any one part of the

beach than another. On the contrary there is positive evidence that the chances of survival are similar on all parts of the stony beach where animals are sufficiently plentiful for an analysis to be made of the population structure. For consider the transect stations 2, 3 and 6, the first two near the lowest high-water mark of neap tides (L.H.W.N.), the last a little below mean tide level (M.T.L.); the numbers of animals of all ages taken at these stations were respectively 2323, 4099 and 2005; first-year, second-year and older animals were present in the three groups in the proportion of

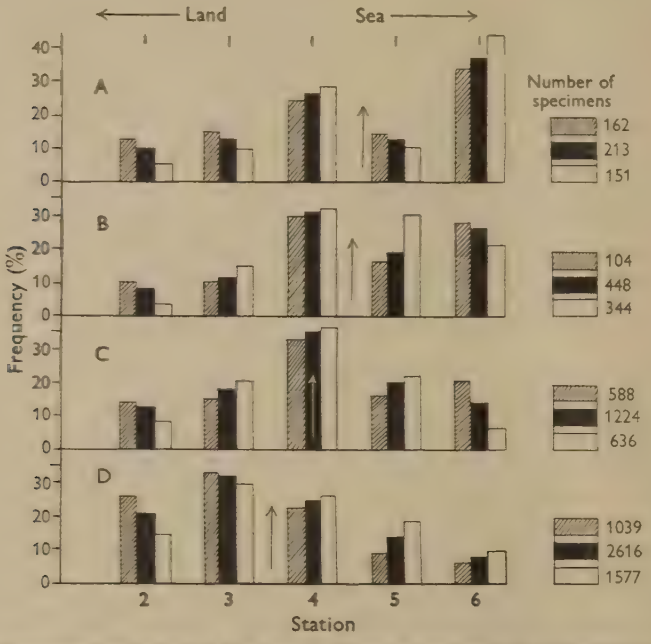

Fig. 3. The frequency distribution of first-year *L. littorea* at stations 2–6. (A) animals of < 5, 5 and 6 mm shell length; (B) 7 and 8 mm; (C) 9 and 10 mm; (D) 11 and 12 mm. The black columns represent the percentage frequency of animals in the twenty collections made over the period October 1951–November 1952. The cross-hatched and unshaded columns show respectively the distribution from October 1951–April 1952 and from April–November 1952. The vertical arrows mark the averaged position (centre of distribution) on the transect of all individuals in each of the four size-groups.

33 : 62 : 5, 32 : 61 : 7 and 31 : 53 : 16, or, taking the ratios of the first- and second-year animals only, 34 : 66, 34 : 66 and 37 : 63. The remarkable similarity of structure of populations of varying densities and drawn from different levels of the shore shows that the mortality-rate and expectation of life is independent of the position of the periwinkles on the shore, at least within the vertical range (L.H.W.N. to M.T.L.) of the particular transect examined. The changes in vertical distribution recorded in Fig. 3 are therefore to be attributed to an actual upshore movement of some at least of the young periwinkles during their first year, a conclusion supported by two further circumstances. The first concerns the size of the smallest animals taken at the various stations, it being notable (Table 4) that the smallest (2·5 mm) periwinkles were found only at

station 10, the lowest of the stations accessible at low water of most tides. Higher up the beach there is a progressive increase in the size of the smallest animals taken and a decrease in the proportion in which they occur in the collections from the different levels. The second indication of the upward movement comes from an examination of samples collected at station 1 at or near the upper limit of occurrence of *L. littorea*. Here there are few animals and they are all comparatively large; the smallest specimen in the samples was 12 mm long. It is evident that animals taken at this station have not spent all their lives there but have moved in at some time from a lower level on the shore. If an upward movement is possible on this part of the beach it is difficult to deny its occurrence at other levels.

Table 4. *Percentages of the size-groups in the collections from different stations*

Station	Smallest animal (mm)	Size-groups ⩽3 mm	⩽4 mm	⩽5 mm
1	12	0	0	0
2	4	0	0·6	0·8
3	3	0·1	0·7	0·9
4	3	0·3	1·7	2·1
5	3	0·4	0·7	0·9
6	3	0·9	2·6	4·6
9	3	2·5	5·0	6·2
10	2·5	6·2	10·0	17·2

THE MOVEMENTS AND ZONATION DYNAMICS OF THE ADULT ANIMALS

The foregoing account has shown that periwinkles when one year old or thereabouts (shell length about 12 mm) are distributed, over a transect which covers the upper half of the middle shore, in their greatest number just below the high-water mark of the lowest neap tides (station 3) the numbers falling off sharply above and below this level (Fig. 3D). This distribution has been further shown to be attained by a progressive movement of the juveniles up the beach during their first year. At the age of 12 months *L. littorea* becomes sexually mature and enters upon adult life. On the Whitstable beach adults were almost always found to outnumber the juveniles, those in their second year, with a shell length of 13–16 mm making up the bulk of the population (Table 3). The vertical distribution of the second-year animals along the transect is shown in Fig. 4 for each of the two groupings 13–44 and 15–66 mm. The similarity of distribution of the two series and of the 11–12 mm class will be evident. In other words, the distribution attained at the end of the first year is preserved virtually unchanged throughout the second year. The maintenance, within a population, of a stable vertical distributional pattern in the face of an apparent freedom of movement of its individual members raises a number of questions bearing on zonation dynamics some of which will now be examined.

There is in the first place no doubt that periwinkles do move about freely, and often extensively, either under cover of the tide or in the open air whenever temperatures are not extreme and the substratum is wet. In an attempt to measure the direction and extent of the movement, the shells of 600 medium-sized *L. littorea* were marked with yellow cellulose paint and placed at a time of spring tides in April when a slight

offshore breeze was blowing and the sea was slight, 100 within a square-metre area at each of the stations 4–6. The extent of dispersion of the marked animals first after one period, and then after three periods of tide cover, is set out in Table 5.

Many of the shells showed signs of having lost some paint by flaking which may account in part for the failure to recover more than a proportion of the marked shells. Some were no doubt overlooked, and a few may have travelled outside the area searched. But in spite of these deficiencies the trials showed clearly, as did those of Dexter (1943), that periwinkles on every part of the beach may undertake considerable excursions, and that no one direction is especially favoured. This is clear from tracks of animals living on the mud flats. Of 112 tracks examined 24 led with much running

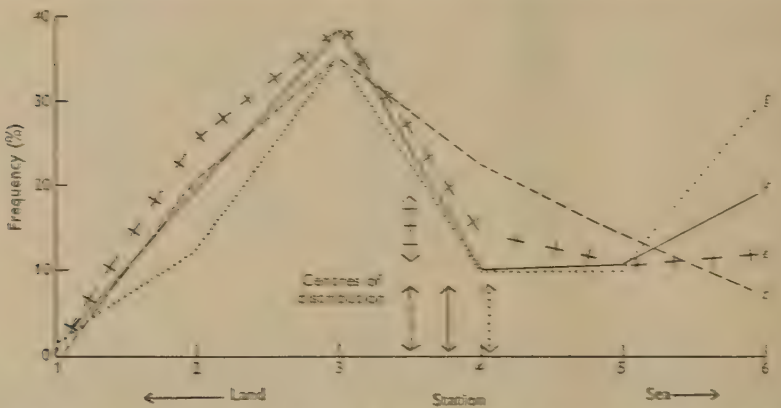

Fig. 4. Frequency distribution of *L. littorea* at stations 1–6. (*c*) 11–12 mm shell length (end of first year—2618 specimens); (*e*) 18–14 mm and (*f*) 15–16 mm (second year—*e*, 3896; *f*, 2616 specimens); (*g*) ⩾ 17 mm (third year and older—804 specimens). The vertical arrows mark the centres of distribution of the groups.

in a general shoreward direction, 38 were to the seaward, 30 led easterly along the shore, and 20 to the west. The maximum speed of movement was about 20 ft h. though the average rate was much lower, for after three hours of tidal exposure few of the tracks were more than about 12 ft long. Because of the circuitous course of the excursions the displacement in a straight line from the original position did not exceed about 8 ft and was, in many instances, a matter of a few inches only. On the stony beach much the same kind of circuitous movement occurs. The animals cannot be continuously viewed here but many which after the passage of one tide had been displaced in a particular direction were found, after re-marking with a paint of a second colour, to have moved after a further period of tide cover in an entirely different direction; some, indeed, had doubled back on their tracks.

We may now return to a consideration of how a distributional equilibrium is maintained in the face of these movements. It is evident that the pattern could be preserved in one of two ways. There could be a virtual segregation of the local populations at the different vertical horizons with the consequent retention during adult life of the distributional pattern attained by the periwinkles at the end of the

first year, or there might be a more extensive mixing of the populations, a stable overall distributional pattern being maintained by differences in the speed of movement and rate of turning at the different beach levels. If the randomness of the movements limits the dispersal of locally aggregated groups to diffusion-mixing then the first alternative is the more probable; if, in spite of the randomness of the movement, dispersal appears to be widespread, the second is to be preferred. In order to find out what is actually happening on the beach it is necessary to have some means of distinguishing between the periwinkles living at the different levels and of keeping the distinctive characteristics under review over long periods. This has, fortunately, been made possible by the fact that periwinkles become subject to natural 'markers' by the

Table 5. *The direction and extent of movement of 100 marked* Littorina littorea *at each of the transect stations 1–6*

The figures show the number displaced in each direction and (in parentheses) the maximum displacement (ft).

Station	No. left in square	After cover of one tide				No. left in square	After cover of three tides			
		S.	N.	W.	E.		S.	N.	W.	E.
1	51	6 (1)	11 (3)	4 (2)	6 (3)	6	3 (2)	27 (20)	6 (8)	15 (18)
2	60	2 (2)	3 (4)	4 (1)	8 (2)	27	8 (4)	3 (2)	11 (7)	5 (7)
3	37	4 (4)	5 (2)	1 (2)	3 (2)	9	7 (7)	2 (3)	5 (6)	0
4	65	2 (½)	6 (2)	2 (½)	3 (2)	18	13 (5)	10 (3)	10 (8)	8 (4)
5	60	11 (2)	4 (1)	0	8 (2)	19	14 (5)	12 (3)	13 (4)	3 (2)
6	70	2 (½)	3 (1)	2 (½)	3 (1)	14	8 (4)	23 (4)	15 (3)	1 (2)
Total	343	27	32	13	31	93	53	77	60	32
Percentage recovered		74					52			

settling upon their shells of other organisms. The distribution of shells on which such organisms are present often gives a clear indication of the direction and extent of the individual and group movements. It was noted, for example, that few of the *Littorina* shells from near the high-water mark were pitted by *Polydora* borings; those on the lower shore, on the other hand, were always considerably excavated. It can be assumed therefore that any *Polydora*-infected periwinkles taken from the higher parts of the beach are likely to have been living, at some time or other, lower down. Algae characteristic of particular levels are equally indicative, when found on periwinkle shells at a level above or below their normal range, of a former displacement. In the present survey the barnacle *Elminius modestus* Darwin was found to be the most consistently useful marker. This cirripede, which has in the past few years almost entirely displaced *Balanus balanoides* L. as the dominant intertidal barnacle of the Thames estuary, is present wherever there are holding stones from low water to M.H.W.N., but on the transect surveyed the density of settlement diminishes rapidly from the mid-tide level upwards (Table 7). If now the shells of adult specimens of *L. littorea* from the different stations are examined, all degrees of cover from barnacle-free to completely encrusted shells are found. In recording the extent of coverage the following categories were recognized (Fig. 5): (0) barnacle free; (1) light cover—up to and including an area of surface equivalent to the shell apex; (2) medium cover—apex to apex plus half of the last whorl equivalent; (3) heavy cover—apex plus half of the last whorl

equivalent to complete cover. A cover factor is then assigned to each sample on the following basis, exemplified in Table 6. The cover density of the different sized individuals is estimated and the numbers of individuals in the four categories 0, 1, 2 and 3 recorded. The products of the number of adult individuals of 13 mm and over in each category, and of their respective cover indices are then summed, the resulting sum finally being divided by the number of individuals in these categories and expressed as a percentage figure.

In 1952, *Elminius* spat began to settle on the Whitstable beach about the middle of April and settlement continued until mid-October. The barnacles grow rapidly at first and not many die or are rubbed off the shells until they are a little over a year old when, after spawning, the old stock dies, falls off the periwinkle shells, and is replaced by new brood. The period of death and detachment lasts from mid-May to mid-August. Any large-scale migrations of *L. littorea* during the winter should therefore be reflected in a modification of the cover factors recorded at the different levels of the

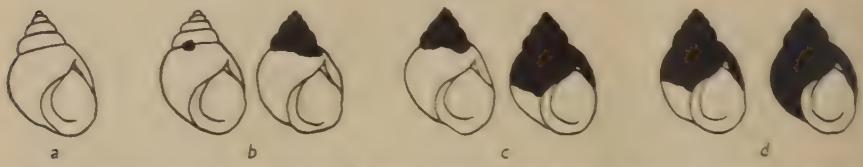

Fig. 5. Variations in the extent of cover of *L. littorea* shells by the barnacle *Elminius modestus* L., and the categories used in estimating the cover factors of populations of *L. littorea* at different shore levels. *a*, barnacle-free—0; *b*, light cover—1; *c*, medium cover—2; *d*, heavy cover—3.

beach in the previous October. The considerable and general detachment of the barnacles during the summer months makes the cover factors less reliable indicators of movement during this period, though they serve as a useful check on possible large-scale migrations. It should be mentioned here that the degree of barnacle encrustation is of little value in plotting the movements of first-year periwinkles. The reason for this is that most of the first-year animals at Whitstable develop from eggs spawned in April and May. *Elminius* cyprids usually fail to attach to *Littorina* shells less than 10 mm long; in fact of 1100 such shells only seven had a barnacle on them. The April–May brood, which provides most of the first-year stock of periwinkles and which are not more than about 5 mm shell length in October, thus escape the barnacle spatfall. The periwinkles continue to grow throughout the winter, attaining a length of about 12 mm by the following April when, as 1-year-old animals entering their second year, they become subject for the first time to invasion by *Elminius* cyprids and receive recognition markings.

The cover factors over the year of the second-year animals from the transect stations 1–6 are set out in Table 7. It has to be borne in mind, when inspecting this table, that some variations in the numerical range of the cover factors from one collection to another (i.e. in the successive vertical columns) are to be expected. The judgement of the extent of cover of individual periwinkles is, at the best, only roughly quantitative and is likely to lead on some occasions either to an overestimation or to an underestimation of the extent of cover, the range of cover factor values determined

for any particular occasion often depending on the standards rather arbitrarily adopted in assigning the first few specimens examined to their respective 'cover categories'. It is therefore the more notable that in the samples 1–10 (mid-October to the end of May), during which period there is no new settlement of *Elminius* spat and very little loss of settled barnacles by abrasion, the cover factors should, except in the two instances marked by brackets, follow the unvarying pattern of a stepped increase in the succession from the bottom to the top station of the transect. The maintenance of a cover-factor pattern with such a constant relation to the spatial distribution of the periwinkle population on the stony beach demonstrates conclusively that there is no general mixing of the populations at the different beach horizons

Table 6. *The estimation of the barnacle cover factor exemplified by samples of* Littorina littorea *collected on 3 October 1952*

	Shell length (mm)							
	13	14	15	16	17	18	19	Total
Station 2								
Total animals	16	17	7	3	1	0	0	44
Barnacle-free (0)	13	16	6	2	1			38
With light cover (1)	3	1	1	1	0			6
With medium cover (2)	0	0	0	0	0			0
With heavy cover (3)	0	0	0	0	0			0

$$\text{Cover factor} = \frac{6 \times 1}{44} \times 100 = 14$$

Station 6								
Total animals	9	19	10	8	4	2	1	53
Barnacle-free (0)	2	0	0	0	0	0	0	2
With light cover (1)	6	13	4	2	2	1	0	28
With medium cover (2)	1	6	5	6	2	1	1	22
With heavy cover (3)	0	0	1	0	0	0	0	1

$$\text{Cover factor} = \frac{(28 \times 1) + (22 \times 2) + (1 \times 3)}{53} \times 100 = 142$$

during winter and spring. The data on the rate of displacement of individual animals, and on the change in the relative value of the cover factors at the different beach levels, were not sufficiently accurate or extensive for a reliable estimate to be made of the degree of mixing of the populations at the different beach levels. Any mixing that does occur appears to be limited to the diffusion which accompanies random movement, and gives no evidence of large-scale directed movements either of an occasional or of a periodic character.

In June and July most of the *Elminius* of the previous year die and fall off the *Littorina* shells. The numerical value of the cover factor thus declines and this guide to the vertical sequence becomes confused and disarranged (Table 7). Once, however, the new spat settles and begins to grow, the earlier sequence again becomes evident, being strikingly similar to that recorded in the corresponding period of the previous year. Except therefore during the short period of June and July, when the barnacle cover is insufficient for a judgement to be made, there is clear evidence that the distribution attained by the shoreward movements of animals during their first year is maintained, in its general features, by the adult animals keeping within the general

bounds of the beach horizons then selected. It seems unlikely under these circumstances that the situation in June and July is different from that at other times of the year.

On the upper part of the middle shore at Whitstable (i.e. on the stony beach) relatively few periwinkles survive beyond their second year; of the adult population on the stony beach only about one-seventh of the total are more than two years old (Table 3). The distribution of the older animals along the line of the transect stations is shown in Fig. 4*g*. Compared with the second year population (Fig. 4*e*, *f*) the centre of distribution has moved a little lower down the beach, but the shift is almost entirely due to the occurrence of the older animals in some number at the most

Table 7. *Density of* Elminius modestus *on stones and on shells of* Littorina littorea *at different levels of the shore* (*Stations 1–6*)

	Stone cover: barnacles per unit area	*L. littorea*: Cover factors of shells > 12 mm long															
		1951				1952											
		21	17	9	30	22	10	24	17	8	18	24	16	9	19	3	11
Station		Oct.	Nov.	Dec.	Dec.	Jan.	Feb.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
1	53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	56	18	34	0	12	14	17	11	4	3	13	16	8	13	14	14	26
3	196	25	72	44	15	39	32	37	27	22	19	8	19	29	36	43	49
4	232	47	108	82	36	33	47	38	74	74	36	16	2	43	50	75	65
5	504	68	120	159	58	71	79	60	111	67	17	25	15	110	96	128	129
6	564	135	224	236	173	177	109	107	124	131	54	40	—	116	146	142	192

seaward station (station 6). Their presence here may be due either to a seaward movement of animals previously living higher up the beach, or to better conditions for survival at station 6 than elsewhere along the transect, or to a movement upshore of older animals from below low-water mark. Large periwinkles from station 6 are always completely covered with barnacles, which seems to rule out the first alternative, but there is not sufficient information available to decide which of the remaining alternatives is the more likely. There is nothing, however, to suggest that the pattern of distribution or the behaviour of the older periwinkles is different from that of the second-year animals.

SOME BEHAVIOURAL IMPLICATIONS

The present survey has shown that on one particular transect of a gently, but continuously sloping stony beach the population of adult periwinkles is distributed in a pattern which remains substantially constant at all times of the year. This pattern which, for clearer illustration, is represented in Fig. 6 by a 'kite' diagram, emerges as the result of a shoreward migration of young animals during their first year and is subsequently maintained by the adult periwinkles which, though usually in movement when the substratum is wet, keep within a fairly well-defined beach horizon. It is justifiable to suppose, in view of these findings, that the environmental factors and features which direct and shape the behavioural movements are in some way related to the orientation and gradient of the transect. But the assumption is valid only if the features are strictly dependent on, and not merely incidental to, the topography of the transect.

There are, for example, on many shores, a number of more or less randomly distributed features such as pools of standing water, isolated clumps of stones or of algae which favour the local aggregation of periwinkles. These might become associated with a particular transect in such a way as to obscure the real significance of the observed distribution. In the area of the present survey stones were rather evenly scattered and algae were virtually absent. There were, however, considerable spatial and temporal variations in the amount of standing water present. The effect of these variations was frequently seen in the numbers of animals taken in the collections. It was shown, for example, in the different population densities of adjacent square-metre areas of ground, there being on one occasion when a count was made (station 2, 19 September 1952) from four to five times as many periwinkles in the wet as in the

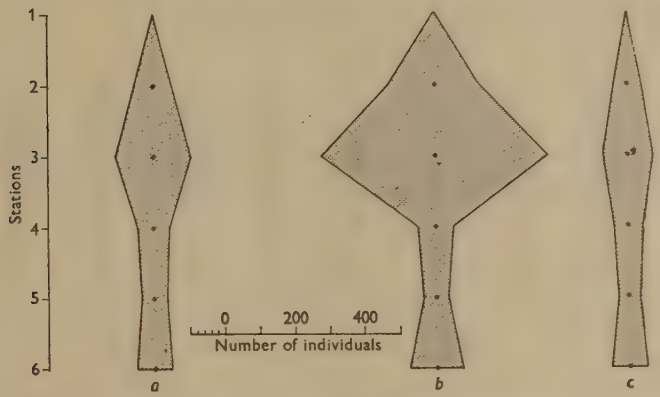

Fig. 6. 'Kite' diagrams of the frequency distribution of *L. littorea* at stations 1–6 of the beach transect. *a*, distribution based on the average number of animals found at each station in twenty collections taken over a period of 13 months; *b* and *c*, variations in the pattern of distribution in successive collections of 1215 and 409 individuals.

dry area. Again, when on successive occasions (3 and 24 June 1952) there is a marked difference in the amount of standing water on the transect the attendant differences in population density are evident (Fig. 6*b*, *c*). Or again, when a particular region is always relatively dry as in the slightly elevated area around station 5 (Fig. 2), fewer periwinkles tend to be found there than at the neighbouring, adjacent stations (Table 1). The question then arises whether drainage conditions may not of themselves be responsible for the observed differences in density of the adult periwinkle population along the transect, or whether, notwithstanding the tendency of animals to aggregate in permanently wet places, beach level is in itself an important (perhaps the most important) factor in determining population density. Time did not allow of the collection and analysis of samples from a variety of drainage conditions at the different shore levels in sufficient number for a quantitative estimate to be made of the significance of vertical position in relation to population frequency. Nor was it thought necessary to do this since there are a number of clear indications that vertical position is in itself relevant to the distribution. The pattern of distribution of the adult periwinkles, is, in the first place, substantially constant at all times of the year in spite

of variations in the distribution of the surface water (Fig. 7). Again, the wettest places do not invariably support the greatest number of animals. There was, usually, for instance, more water present at station 6 than at station 3, and yet on sixteen out of the twenty occasions when collections were made from both places (Table 1), the number of periwinkles taken at the higher and drier level was greater, often very much greater, than at the lower, wetter level. Finally, and perhaps most significant of all, is the fact that when the extent of barnacle cover of *L. littorea* from the different levels is worked out over a succession of collections, the cover factors always reflect the particular level from which the samples are taken, even though the number of animals in the successive samples varies in accordance with the wetness or dryness of the areas from which they are taken. In other words, although wet places are the more favoured, periwinkles do not move up and down the beach to find them, but seek them within the bounds of their own particular beach horizon.

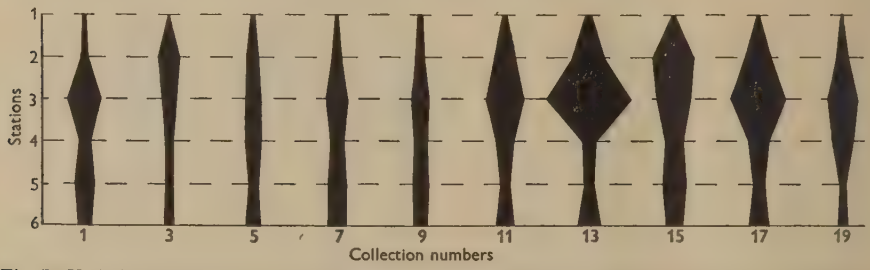

Fig. 7. Variations in the pattern of distribution over the period of 13 months as seen in the succession of samples of odd number 1–19.

The present survey has not been concerned with the identification of the factors and circumstances which contribute to the emergence and maintenance of the zonation pattern characteristic of *L. littorea*. It does, however, confirm the relevance of features having a vertical alignment or distribution in the directing of the behavioural movements which bring about a beach zonation. It shows too that the kinds of stimuli and situations to which periwinkles respond are conditioned, to a large extent, by the age of the animals. In particular, the shoreward movement of the young periwinkles during their first year suggests that 'token' stimuli having directional attributes are important to them, their movements thereafter being more closely adapted to the immediate means of existence. The sequence of behavioural responses of *L. littorea* is, on an extended scale, reminiscent of the events by which, for example, zooplanktonic organisms responding to the stimulus of light are brought, by vertically directed movements, into regions rich in phytoplankton, to the subsequent exploitation of which their more randomly conducted behavioural movements are then directed.

SUMMARY

1. The common periwinkle, *Littorina littorea*, has been shown by a number of previous workers to have an intertidal distribution with a sharply defined upper limit, a less sharply defined lower limit, and a distribution over the middle shore (Yonge 1949) in which it is more numerous at some levels than at others.

2. In order to study the way in which this zonation emerges and is maintained collections were made at Whitstable at 3-weekly intervals over a year along a line of stations spanning a transect of a gently sloping stony beach covering the upper half of the middle shore (M.T.L.–M.H.W.N.). Offshore plankton samples were also examined to determine the availability of new stock.

3. Pelagic post-metamorphic juvenile periwinkles are most abundant in the Whitstable plankton from April to June, but are present at all times of the year; the planktonic young do not exceed 0·25–0·5 mm in length.

4. The smallest *L. littorea* found on the shore had shells 2·5 mm long and the population never contained more than 4% of animals shorter than 5·0 mm. It is therefore argued that the population on the beach is continually recruited from the sea bottom below low-tide mark.

5. Young littorinids are readily transported by wave action over the almost level 'flats' of the lower reaches of the Whitstable beach, and ultimately reach the lower margin of the stony beach. There is a further shoreward movement of the young *L. littorea* over the stony beach during the first year of life, and these movements are mainly locomotory and not due to wave action.

6. The adult zonation is achieved at the end of the first year. Thereafter the distributional pattern of the adults remains substantially constant at all times of the year and throughout the life of the adult periwinkles.

7. By measuring the extent of settlement of the barnacle *Elminius modestus* on the periwinkle shells from different beach horizons it can be shown that the zonation pattern is dynamically maintained. Periwinkles remain, on the whole, at the beach horizon which they had attained at the end of the first year.

8. Patchiness of distribution of *L. littorea* due to their tendency to aggregate in wet places is discussed in relation to vertical zonation.

9. Some behavioural implications of the observed distribution of *L. littorea* on the beach are discussed.

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FACTORS INFLUENCING POPULATION FLUCTUATIONS OF *URCEOLARIA MITRA* (PERITRICHA) EPIZOIC ON FRESHWATER TRICLADS

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(With 4 Figures in the Text)

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INTRODUCTION

The regulation of animal populations forms one of the primary interests of ecologists, and at the present time theory is far in advance of practical demonstrations. Before firm conclusions can be reached many more studies of different organisms are needed. The main object of this study is to determine the basis of the regulation of a freshwater epizoic protozoan. Although Protozoa have figured in many community surveys and indeed their population fluctuations have been recorded often, firm conclusions on this aspect have never been reached. Under the stimulus of the applied problems of water purification emphasis has usually been placed upon the various types of community and succession in relation to the progress of purification.

Urceolaria mitra Von Sieb lives upon the dorsal surface of freshwater triclads, especially *Polycelis tenuis* Ijima. In a preliminary paper (Reynoldson 1950), the suitability of this organism for a study of the factors concerned with population fluctuations was pointed out. The early work indicated that rainfall was the most important abiotic factor involved, and Taylor's study (1940) at Windermere suggested that it may operate by increasing the number of bacteria, assumed to be the food of *Urceolaria*. The main purpose of this paper therefore is to examine the relationships between rainfall and the bacterial population and between the fluctuations of bacteria and *Urceolaria*. An appraisal of these has been assisted by studying the feeding method of *Urceolaria*, the composition of its food and also the influence of predators, parasites and competitors. It must be emphasized that here only *average* population levels are dealt with and not the events within the urceolarian populations of individual worms. The latter forms a vital part of the study but lies outside the scope of this contribution.

Criticism might be levelled against certain conclusions reached in this paper on the grounds that other effects of rainfall, particularly changes in the physical and chemical properties of the medium might influence *Urceolaria*. But it seems clear from ecological studies of ciliates summarized by Noland (1925) that these organisms are very tolerant of such factors as oxygen tension, mineral content, pH, etc. He showed that food is the most important factor controlling their distribution. It was felt therefore that more useful data would be obtained by concentrating on this aspect of the rainfall study.

The initial observations (Reynoldson 1950) were confined to a small pond in the College grounds. For the present purpose they were extended to another pond subject to similar weather conditions about four miles to the east on the Vaynol Estate, mainly to examine the degree of synchronization of fluctuations in bacteria and *Urceolaria*. Weekly data of population fluctuations for both types of organism were obtained at each locality over a period of twelve months during 1948–49. They were supplemented by daily records of water temperature and rainfall.

A COMPARISON OF THE VAYNOL AND COLLEGE PONDS

College pond has already been described (Reynoldson 1950). Vaynol pond is artificial, but has been in existence about 60 years. It lies over a narrow belt of carboniferous limestone in the midst of good farming land. It is shallow, not exceeding 2 ft in depth, and triangular in shape, measuring approximately $30 \times 65 \times 50$ yd. There is no inflow; water must drain from rising ground which surrounds it. A constant maximum depth is maintained by a weir set in one side over which water can flow into a much larger pond. The weir side of the pond is formed by a concrete coping, the top of which is at ground-level. A concrete base extends into the pond for about 10 in, forming a hard substratum. Elsewhere there is a soft, non-stony mud bottom covered at the edges with a thick seasonal carpet of decaying leaves. The pond is surrounded on all sides by deciduous trees and is consequently heavily shaded in summer. This reduces the summer evaporation rate and helps to maintain the water-level. The pond has never been observed in danger of drying out. A species of *Chara* is the main plant, and during the summer it covers the substratum except within 2–3 ft of the edge.

As shown in Table 1, there are distinct chemical differences between the two ponds, particularly in calcium content. The degree of shading of the two ponds also differs, and results in an absence of emergent and floating vegetation in Vaynol and a rich flora of this type in College pond (Reynoldson 1950). These contrasts are reflected in the fauna, and certain broad differences are unmistakable, particularly in the triclads, leeches and molluscs. For example, the addition of *Dendrocoelum lacteum* (Müll.) to the permanent fauna of Vaynol is the main difference in the triclads. Nevertheless, there was a much greater number of flatworms in College pond, probably associated with the additional, more favourable substrata of stones and plants. The most distinctive differences were found in the leeches and molluscs. The larger number of leech species (five as compared with one) in Vaynol may result partly from the more varied mollusc fauna and partly, e.g. *Theromyzon tessulatum* (O. F.

Müll.) and *Hemiclepsis marginata* (O. F. Müll.) from the presence of water fowl. There are seven species of snail in Vaynol and four in College pond. The presence of *Bithynia leachii* (Sheppard) is noteworthy as a hard-water species (Macan 1949). Despite this the number and biomass of snails was greater in College pond, mainly owing to the large population of *Limnaea pereger* (Müll.) there. This again probably derives from the more abundant vegetation in College pond. The general conclusion, which may have a bearing on the urceolarian problem, is that while the more eutrophic Vaynol pond shows a greater variety of certain groups the number and biomass of organisms are greater in College pond.

Table 1. *A comparison of the chemical properties of College and Vaynol pond water (mg/l.)*

	College Pond	Vaynol Pond
pH	8·25	7·90
Dissolved solids	254·0	442·6
Ca''	15·9	68·1
SO_4''	52·0	23·9
Cl'	33·0	59·0
Hardness (Wanklyn)		
Total	155·0	285·0
Permanent	130·0	105·0
Temporary	25·0	180·0

METHODS

(*a*) *Meteorological records*

Daily records of rainfall were kept for Bangor. Separate records were not obtained for the Vaynol area which is only four miles distant. Daily records of the maximum and minimum water temperatures for College pond were maintained. A similar record could not be conveniently obtained for Vaynol pond, but comparison has been made over a short period during a cold spell and during the summer (Table 2). These figures suggest that in winter Vaynol pond is slightly colder than College pond. During

Table 2. *Comparison of pond temperatures* (° C)

	Max.	Min.	Av. max.	Av. min.	Av.
Winter—21–26 Jan. 1950					
Vaynol pond	5·0	1·7	4·5	3·3	3·9
College pond	6·7	3·6	5·6	3·9	4·7
Summer—29 Aug.–2 Sept. 1952					
Vaynol pond	17·2	13·3	16·2	13·7	15·0
College pond	17·8	12·8	16·8	13·2	15·0

the period of observation the Vaynol pond had a thin ice cover for the whole eight days, while College pond was free of ice for six of the days. During the summer there is probably little difference in average temperature, but College pond tends to have slightly higher maximum and lower minimum temperatures. It is likely that College pond warms up in the early summer rather more quickly than Vaynol pond owing to direct access of sunlight. However, for purposes of relating temperature to population

trends in bacteria and *Urceolaria*, the differences between the two ponds cannot be important, but the greater amount of light reaching College pond may influence chlorophyll-containing organisms.

(*b*) *The estimation of bacteria*

Bacteria may be counted either directly, which affords quick results, or by plating which is more laborious. Taylor (1940) concluded that with present techniques plating was the more reliable. This method was therefore used, although its limitations are clearly recognized. Very recently (Skinner, Jones & Mollison 1952), the two methods have been compared for soil bacteria determinations and here the plate method has not shown up well, mainly apparently due to the difficulty of overcoming clumping. However, this problem is not so serious in determining aquatic bacterial populations.

Table 3. *Bacterial data—analysis of variance*

Source of variation	Squares	Degrees of freedom	Variance
		College pond	
Between pairs	3·877	42	0·092
Within pairs	0·224	42	0·005
		Vaynol pond	
Between pairs	5·199	47	0·111
Within pairs	0·408	47	0·009

For estimating the number of bacteria, weekly samples were taken from both ponds. Sterilized, glass-stoppered 6 oz bottles were used in a sampling apparatus with remote control to avoid contamination. Two samples were taken on each occasion and one plating made from each within one hour of collecting. It was considered that this duplicate sampling would afford a better basis for testing reliability than making duplicate plates from a single sample. In taking the sample approximately one-fifth of the bottle was filled from each of five different areas in the flatworm sampling site. The culture medium used was that advocated by Taylor (1940) except that on his advice (personal communication) casein was used instead of sodium caseinate which was unobtainable at the time. The composition of the medium was as follows: peptone (B.D.H.) 0·5 g, casein 0·5 g, soluble starch 0·5 g, glycerol 1·0 ml, K_2HPO_4 0·29 g, $MgSO_4$ 0·05 g, $FeCl_3$ trace, agar 15·0 g, distilled water 1000 ml. Dilution 1:100 was found most generally useful and used throughout. The plates were incubated for 14 days at 18° C. Trouble from contaminants was slight and only three plates out of 150 had to be discarded.

Foot & Taylor (1949) have shown that this medium gives a satisfactory overall picture of the bacterial population and does not reflect variations in a specialized group. An analysis of variance made for each pond on data converted to a logarithmic basis showed that real fluctuations in the bacterial population occurred (Table 3). The variance ratios are 17·33 ($P < 0·01$) and 12·74 ($P < 0·01$) for College and Vaynol ponds respectively. The difference between pairs, i.e. change with time, is significantly greater than the difference within pairs. The sampling standard error of the mean of a pair of counts was about 15%. Graphical examination also showed a very close

agreement in the fluctuations of each pair for both ponds. On this evidence it seems reasonable to conclude that the bacterial data gave a true indication of population changes.

(*c*) *The estimation of* Urceolaria

The method used to determine the *Urceolaria* population in College pond, on the basis of number per worm, has been described and shown to give a reasonable estimate (Reynoldson 1950). Briefly, it consisted of making a random collection of twenty worms on one day in each week, and counting the number of *Urceolaria* on them. For ease in counting, the flatworms were placed in a drop of 0·02% chromic acid on a well-slide, for 10–15 min. The detached urceolarians were then counted under a binocular microscope. Any examples of binary fission or conjugation were confirmed by microscopic examination and noted. The flatworms recovered on being put back into pond water. This method was continued during the present work with one minor difference: worms recognizable by their pigmentation and size as being recently hatched were not collected. They were neglected because it had been shown (Reynoldson 1950) that the size of the urceolarian population is distinctly lower than the average value in the case of young worms less than approximately 4·0 mm in length. Any young individuals which evaded this screening were discounted in later calculations. In practice this amounted to omitting data for less than 1% of the total worms examined.

A similar method was used for Vaynol pond, but here the sample size was increased to twenty-five worms to allow for infrequent specimens of *Polycelis nigra* which were sometimes collected in mistake for *P. tenuis*. In the case of College pond its proximity enabled such errors to be righted by further collecting. Also with the Vaynol collections it was necessary to count the epizoites under the microscope initially because of difficulty in distinguishing *Urceolaria mitra* from *Trichodina steinii* which also lived on these flatworms. After experience it was possible to identify reliably with the binocular under most conditions. An analysis of the relationship between the length of the flatworm and its *Urceolaria* population suggested that worms 4–5 mm in length should be omitted in the Vaynol population. The average population of *Urceolaria* per worm in Vaynol pond was approximately five times that in College pond over the period of observation. The variance of the population in the two ponds was compared by examining the standard deviation of twelve pairs of samples, three selected at random for each season. Expressed as a percentage of the mean, the average value for College pond was 64·7%, with a range of 103·3–35·5% and for Vaynol 60·0% with a range of 87·8–48·6%. Thus the estimates of the *Urceolaria* population in each pond may be regarded as comparable.

The flatworms from Vaynol were returned to the pond on the following week at a point farthest from the collecting site. The population of triclads in this pond was not as great as the College pond population, and the danger of invalidating results by depletion of the worms was considered greater than that of any possible dilution effect upon the *Urceolaria* population. This decision was based on the relative reproductive rates of Protozoa and flatworms.

The sampling was staggered over the week to spread the routine work. For College

pond bacteria and *Urceolaria* were sampled with a two-day gap, for Vaynol on the same day. This has meant a slightly different treatment of the data when fluctuations of the two organisms are compared.

(*d*) *Analysis of the data*

In analysing the data the method of correlation, with certain refinements, has been largely used. In the case of bacteria the two weekly samples were averaged and a log n transformation used because of the wide range of values from week to week. For all calculations involving *Urceolaria* a log $(n+10)$ transformation of the individual counts was used to destroy the close linear relationship between the sample mean and its standard deviation.

Table 4. *Comparison of rainfall incidence with fluctuations of bacteria and* Urceolaria

	Rainfall (3-day average)	Bacteria per ml	*Urceolaria* per worm
13 July	Nil	7150	21·2
16 July	0·27	50100	20·2
20 July	0·03	5200	25·1
23 July	0·35	—	17·9
27 July	0·07	17000	20·7

Some difficulty was experienced in arriving at a suitable basis of comparison for the bacteria-*Urceolaria* trends within and between ponds, partly because of an evident lag in reaction by *Urceolaria* to bacterial changes which also varied seasonally, partly because of time differences in sampling. A short period of three-day observations for College pond (Table 4) afforded evidence on the reaction period of *Urceolaria* under summer conditions. The daily rainfall preceding the *Urceolaria* count was 0·02, 0·27 and 0·53 in. for 14, 15 and 16 July respectively. These data suggest that the bacterial population would show a marked increase about 36 h before the urceolarian population was sampled on the 16th. Yet at this time the latter showed no response. Four days later (20 July) the epizoic population showed an increase, which of course may not have been its peak. The population had declined by 23 July. It seems likely that if *Urceolaria* responds to bacteria this reaches a peak after 3–4 days in summer. Under winter conditions it has been shown that there was an even greater delay in reaction by *Urceolaria* to rainfall (Reynoldson 1950) which was also apparent in the present work in relation to bacteria. Therefore, to take account of both the lag in reaction time which varied with the season and the sampling differences, the following procedure was adopted based on earlier experience. For College pond when the temperature was $\geqslant 12{\cdot}5°$ C the data for *Urceolaria* were related to the bacterial data for three days previous; when the temperature was $\leqslant 12{\cdot}5°$ C to the bacterial data for ten days previous. For Vaynol pond the *Urceolaria* data were related to the bacterial data averaged for the day of sampling (= week 0) and seven days previous (= week 1) in the warmer months and to the average of weeks 1 and 2 in the colder months.

A GENERAL COMPARISON OF THE URCEOLARIAN POPULATIONS

The comparison is based mainly on the epizoic population of *Polycelis tenuis* but a few *P. hepta* Melander (Melander, Melander & Reynoldson 1954), which has a similar population, may be included. The average number of *Urceolaria mitra* per worm in College pond over the period of observation was 10·2, S.D. ± 8·42 (847 flatworms); for the Vaynol population the corresponding value was 56·2, S.D. ± 34·00 (917 flatworms). Thus the Vaynol population of *U. mitra* is approximately 5·5 times larger than that of the College pond. Taking the populations over the whole period the averages are very significantly different ($t = 38{\cdot}3$, $P < 0{\cdot}001$). In a comparison of twelve pairs of weekly samples selected to cover the range of fluctuations, the means were all significantly different with values of t ranging from 3·12 to 8·39 with $P < 0{\cdot}005$. Thus it is clear that there is a consistent and well-marked difference in the population densities of *U. mitra* in the two ponds.

Table 5. *Frequency distribution for* Urceolaria *on individual worms*

Number of *Urceolaria*	College pond	Vaynol pond
0–9	500	18
10–19	222	64
20–29	93	109
30–39	29	126
40–49	3	121
50–59	0	119
60–69	0	105
70–79	0	79
80–89	0	49
90–99	0	44
⩾100	0	80

The range in numbers of *U. mitra* on individual worms was 0–48 for College pond and 0–275 for Vaynol. In the latter case only one worm was collected without epizoites. Table 5 compares the frequency distributions of the two populations. The maximum and minimum average weekly values of *U. mitra* for College pond were 25·1 and 2·2 per worm; for Vaynol, 93·2 and 26·7 per worm. These represent absolute maximum ranges of 22·9 and 66·5 respectively, while the relative ranges based on minimal values are 11·4 and 3·5 respectively. Thus the College pond population showed a lesser absolute but a greater relative amplitude of population fluctuation.

Over a host size from 4·0 mm length and upwards the College pond population of *U. mitra* is independent of host size during most of the year (Reynoldson 1950). This greatly simplifies the analysis of population fluctuations and initially a similar assumption was made for the Vaynol population. However, when the relationship was examined (Fig. 1) it was clear that worms less than 5·0 mm in length had a markedly lower epizoic population than the rest; to a lesser extent this was also true of worms up to 6·0 mm in length. The high value for *Urceolaria* infesting the largest worms is based on only twelve counts which may not be representative. A comparison of the 4·5 mm category with the larger worms showed a mean of 32·5, S.D. ± 21·20, compared with 56·2, S.D. ± 34·00, the difference between the means being highly significant

($t = 5{\cdot}06$, $P < 0{\cdot}001$). Over the range of host size 5·0 –11·0 mm length, the epizoic population showed no significant increase. The correlation coefficient for host size–epizoic population excluding worms less than 5·0 mm length was 0·129, $P > 0{\cdot}1$. Assuming an equal host growth-rate, it seems that the flatworms in Vaynol pond become infested at a later stage than in College pond. This is likely in view of the smaller host population in Vaynol pond, but it ignores any influence of crowding of *U. mitra* upon dispersal rate, a point which has yet to be examined. For the present purpose it is clear that in determining average *Urceolaria* populations worms less than 5·0 mm length should be omitted. This has been done, but in practice has made little difference because there were only 54, 6% of the total (968).

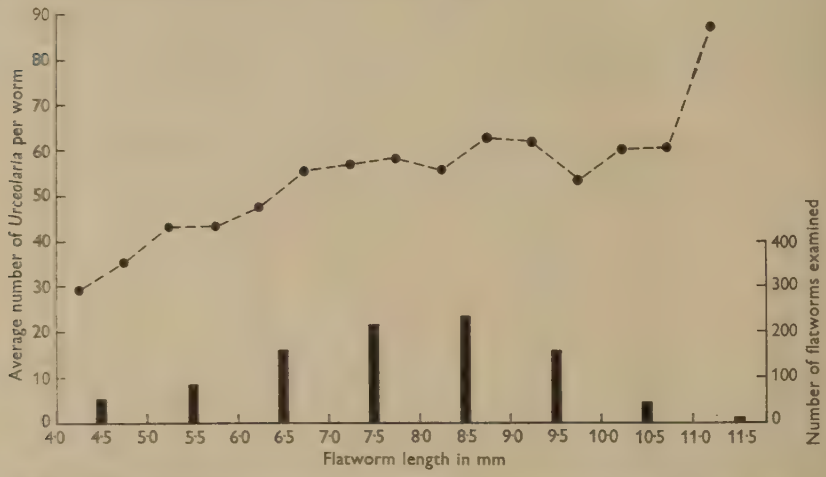

Fig. 1. The relationship between host size and the *Urceolaria* population for Vaynol pond.

Observations have also been made on certain aspects of the life history of *U. mitra*. Individuals undergoing binary fission were observed on seventy-six occasions in Vaynol specimens and on only two occasions in College pond specimens. Not only was binary fission more frequent on an absolute basis in the Vaynol population, but also on a relative basis when corrected for the number of *Urceolaria* examined. In the Vaynol population, it represented an average of 19·5 per 10000 specimens and in College pond 2·3 per 10000 specimens. However, examples of binary fission in College pond populations were so few that the calculated rate must be accepted with reserve, but it can be concluded that the Vaynol population showed a higher reproductive rate. Individuals in conjugation were also noted on thirty-three occasions in Vaynol specimens and five in College pond individuals. On a relative basis this does not represent a great difference, 7·6 and 5·8 per 10000 respectively. The seasonal occurrence of the phenomenon is interesting, since apart from one example (24 April 1949) from Vaynol, it was confined to the warmer period of the year (June to the beginning of November) when the water temperature was above 11·5° C. The five examples from College pond were confined to one sample in July.

It is not proposed to discuss the *Urceolaria* populations of the other flatworm species living in the two ponds. The marked host specificity already demonstrated for *U. mitra* (Reynoldson 1947, 1948, 1950) was also apparent in the Vaynol pond where the epizoites occurred most abundantly on *Polycelis tenuis*; *P. nigra* and *Dugesia lugubris* had by comparison extremely small epizoic populations. The incidence of infestation of the latter two species will be examined in a later paper dealing with host specificity.

Table 6. *The* Urceolaria *populations of flatworms heavily infested with* Trichodina steinii

	Numbers on individual flatworms.		
	T. steinii	*U. mitra*	Average *U. mitra* per sample
1948			
9 Sept.	64	57	63·0
15 Oct.	60	18	37·4
26 Nov.	96	75	81·0
1949			
30 Mar.	90	81	54·0
13 June	54	53	72·0
27 June	73	48	53·0
18 July	327	40	45·4
	102	47	
24 July	74	63	50·0
	79	29	
	145	50	
	221	28	
1 Aug.	70	32	51·9
	77	84	
	80	56	
	82	78	
	93	69	
	104	9	
	116	124	

The presence of the related *Trichodina steinii* C. & L. on the Vaynol *Polycelis tenuis* introduced an additional complication. Although the interaction of these two species provides an intriguing study yet to be attempted, the present purpose is to show that in Vaynol pond *Trichodina steinii* did not influence *Urceolaria mitra* in any important way. The grand average population of *Trichodina steinii* was low, 5·1 per worm, compared with 56·2 per worm for *Urceolaria mitra*. Using fortnightly averages the range for *Trichodina steinii* was 0·1–41·3 per worm—excluding the largest value, it was 0·1–9·5. The seasonal trend showed a general similarity to that of the *Urceolaria* population, except that there was a sudden increase in July. When all the data are included correlation between the trends is not significant ($r = -0{\cdot}001$, $P > 0{\cdot}1$). But if the probably abnormal July value of 41·3 for *Trichodina steinii* is omitted the correlation is significant ($r = +0{\cdot}426$, $0{\cdot}02 < P < 0{\cdot}05$). This evidence suggests that interaction between the two species, if occurring, does not obliterate the effect of other environmental factors. Insufficient is yet known about the biology of *T. steinii* to take the argument further. The epizoic populations of individual worms with a relatively high population of *T. steinii* ($\geqslant 50$) are recorded in Table 6. There are ten cases where

the number of *Urceolaria mitra* is less than the average for the sample and nine where it is equal to or greater than the average. Also in the data for 24 July and 1 August there is no tendency for the population to become progressively reduced as the *Trichodina* populations increase. Thus, the presence of *T. steinii* did not depress the population of *Urceolaria* and seemingly it may be ignored in this context.

THE INFLUENCE OF HOST ABUNDANCE ON THE URCEOLARIAN POPULATION

Clearly, if host fluctuations affect the epizoic population correction of the *Urceolaria* data would be necessary. There are so many factors complicating this relationship (e.g. localized distribution and aggregation of host, the volume of water fed to the epizoite) that it is difficult to devise realistic experiments. By chance, the best evidence on the problem was obtained in 1952 following a drastic reduction of the host in College pond.

To assist the planning of experiments the seasonal fluctuations and density of *Polycelis tenuis* were assessed in each pond but different techniques had to be used because of the substrata. In Vaynol a 6 in. square frame was placed at random on the concrete bottom, the debris within collected and the worms sorted out. Three such

Table 7. *Population fluctuations of* Polycelis tenuis

	College pond (number per tile)	Vaynol pond (number per 36 in²)
1949		
Apr.	55	6
May	48	—
June	40	10
July	59	19
Aug.	38	27
Sept.	—	26
Oct.	22	6
Nov.	15	27
Dec.	13	28
1950		
Jan.	17	12
Feb.	13	11
Mar.	10	—
Apr.	25	7

samples were taken on one day each month. In College pond with its vegetation and soft substratum, three tiles were placed at monthly intervals, left for one week and the number of attached worms counted. The Vaynol method gave a quantitative estimate and seemed reliable, the results conforming to the impression gained by the weekly visits. Here, the population was small enough for the increase due to early summer breeding to be detected (Table 7). The College pond method was relative only and probably gave a picture of activity rather than abundance. The weekly visits suggested that the fluctuations in College pond were less than in Vaynol, although the data do not show this (Table 7). In the latter the maximum range was of the order of 5 × but variations took place gradually and with the exception of one dubious result the maximum change from one month to another was about 2 ×.

Experiments were made to see if such variations in host abundance influenced the *Urceolaria* population by keeping a constant number of worms in different volumes of water and counting the epizoites after one week. The method is extremely artificial, but in some respects was a severe test for inter-host competition. The number of hosts per volume of water was chosen to cover rough approximations of 5 per litre in Vaynol pond and 25 in College pond. Five worms, selected for similarity in size and epizoic population, were used in each vessel. A single large sample of water from College pond was apportioned between Pyrex containers of such a size as to keep the area : volume ratio approximately constant. The experiment was repeated three times with similar results, the average percentage distribution of total *Urceolaria* (4300) between the dishes being 19·2, 21·1, 23·2, 15·2 and 21·3 in water volumes of 1000, 500, 200, 100 and 50 ml respectively. This shows no evidence of competition, but the results cannot be applied to natural conditions without reserve. However, an opportunity of obtaining much more reliable evidence under natural conditions occurred in 1952. *Polycelis tenuis* had been steadily removed from College pond since 1946, particularly during 1951–52 when large numbers were needed for feeding experiments. This resulted in a sudden catastrophic decline in April 1952, and from being the most numerous species *P. tenuis* became the least numerous. Before the decline the ratio of *P. tenuis*:*P. nigra*:*Dugesia lugubris* was 5:1:2. Three counts involving 250 worms in April 1952 gave the ratio as 0·3:1:2. There was no evidence of a change in the population of *D. lugubris* and if this species is regarded as constant then it appears that the *Polycelis tenuis* population declined by about 95%. If competition between epizoic populations was occurring a sharp increase in *Urceolaria* per worm would be expected. Estimates in April 1952 showed average values of 20·5 and 14·0 *Urceolaria* per worm—well within the range of previous values. This evidence is regarded as proof that the variations of host abundance encountered do not materially influence the epizoic population, nor can the difference in host density in the two ponds account for the difference in the epizoic populations.

FLUCTUATIONS OF THE BACTERIAL POPULATIONS

The small size of ponds exposes their bacterial populations to more outside influence than those of lakes (for references see Zobell 1946) and they are more likely to be affected by local conditions. A number of factors will modify the influence of rainfall on pond bacteria, e.g. the large, short-period fluctuations of the soil population (for references see Taylor 1936), incidence of rainfall as determining the accumulation of debris, intensity of rainfall in relation to disturbances of bottom sediment, the crumbling of soil during a dry period (Gray 1951*a*), the growth and mortality of indigenous bacteria. Some will intensify, others mask the effect of rainfall on the population making the measurement of the relationship by statistical methods alone unsatisfactory. For this reason the values are shown graphically (Fig. 2) for both ponds. The three-day rainfall averages gave the best agreement, although the seven-day figures were little inferior. The values for bacteria represent the averages of the two samples plotted as logarithms. This basis was used because of the wide range of values. The absolute ranges over the period of observation were 3·5–51·0 thousands

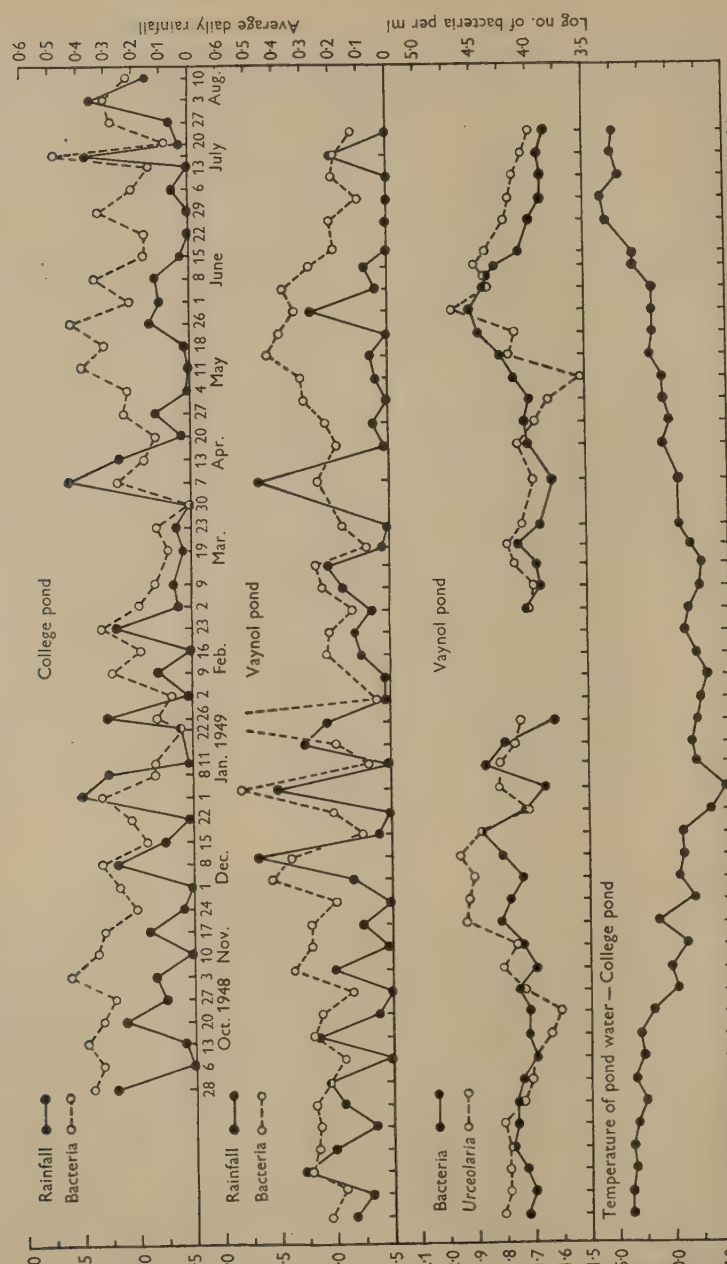

Fig. 2. Rainfall and bacterial fluctuations in the two ponds: also fluctuations of bacteria and *Urceolaria* in Vaynol pond.

per ml for College pond and 2·6–174·9 thousands per ml for Vaynol pond. The much wider range for Vaynol was due to the figure for 24 January 1949. If this is omitted the range becomes 2·6–66·2 thousands per ml. The average values over the whole period (omitting 24 January) were also similar, viz. College pond, 15·19 thousands per ml, Vaynol 13·84 thousands per ml. From the situation of the two ponds a higher count might have been expected in the Vaynol pond. Zobell (1946) notes that the microflora of lakes differs qualitatively from that of the surrounding terrain and inflowing streams, particularly with regard to chromogenic bacteria which in Lake Mendota (Snow & Fred 1926) amounted to about half the total, whereas in the surrounding soil they formed only one-tenth of the total. In the Bangor ponds the chromogenic species formed 15·1% (College pond) and 19·2% (Vaynol) of the total. This might indicate a higher proportion of soil forms. In general the Vaynol species were the more brilliantly pigmented.

The sample taken on 24 January showed a bacterial content about three times larger than the next largest and more than ten times larger than the average. Moreover, at the time of sampling the water had a grey-white opacity so that it was impossible to see the bottom of the pond. A concentrated sample showed a high number of bacteria but was otherwise not unusual. In appearance, the water had all the characteristics of dilute, domestic sewage. Within four days the pond had cleared and apparently returned to normal. Such a phenomenon was never observed at any other time. The probable cause was seepage from a pipe carrying sewage from the estate buildings which ran a few feet from the pond. It seems certain that this was an isolated event following a short period of exceptionally heavy rain. Therefore the figures for this sample have been omitted from all calculations.

Table 8. *Correlation coefficients for temperature, rainfall and bacteria*

	Vaynol pond			College pond		
		Eliminated			Eliminated	
Relationship		Temp.	Rainfall		Temp.	Rainfall
Bacteria-rainfall	0·448***	0·456***	—	0·326*	0·370**	—
Bacteria-temp.	0·017	—	0·091	0·233	—	0·295*
Rainfall-temp.	−0·142	—	—	−0·133	—	—

*** $P<0·01$; ** $0·01<P<0·02$; * $0·02<P<0·05$; absence of asterisk indicates non-significance. These conventions are also used in the text.

From Fig. 2 it is obvious that rainfall produces a marked numerical effect upon the bacteria, in both ponds. This relationship and also any influence of temperature have been examined statistically by calculating correlation coefficients (Table 8). Those involving rainfall are not complicated by serial dependence (Moran 1949, 1952) since the serial correlation coefficient is not significant ($r=-0·217$, $P>0·1$). The results for both ponds show a highly significant relationship between rainfall and bacteria which persists when the influence of temperature is eliminated. It follows from the proximity of the ponds that if rainfall (or any other weather condition) is operative, then the two populations should be in phase. Comparison of the data is complicated because of a two-day gap in sampling but this has been minimized in two ways. By

using a fortnightly average to smooth out differences, and by omitting five of the thirty-eight weekly comparisons when rain intervened between sampling. The values for r were then 0·672*** and 0·555*** respectively. However, the successive values for neither set of data are independent as shown by significant values for the serial correlation coefficients. On the advice of Mr M. J. R. Healy, the values of r were re-calculated using departures from a moving average of groups of five to eliminate seasonal trends. They remain significant, fortnightly $r = 0{\cdot}518$*, weekly $r = 0{\cdot}630$***. It seems conclusive that fluctuations in the two ponds were in step, supporting the view that rainfall was the ultimate cause of the fluctuations. The value of r for the bacteria–temperature relationship is not significant for Vaynol; for College pond it becomes just significant when the influence of rainfall is eliminated. This contrast is due partly to the higher bacterial population in October and partly to the lower value in November and December 1948 for College pond (Fig. 2). The reason for this slight difference between the ponds is unknown. In both ponds a persistent increase in bacteria occurred during May unaccompanied by rainfall which might represent a seasonal growth of indigenous bacteria.

The daily rainfall records showed that bacteria reacted to rainfall certainly within 48 h and probably within 24 h. Fig. 2 also suggests that the increase in bacteria following rain was short lived. This is supported by one series of samples taken at shorter intervals. On 13 July 1948 the bacteria were recorded at 6700/ml; following 0·52 in. of rain on the 15th the population reached 50 100/ml. on 16 July. Four days of dry weather followed and on the 20th the population had fallen to 5200/ml. It is this transitory effect which results in the rainfall pattern impressing itself so markedly upon the bacterial population.

THE BACTERIA–*URCEOLARIA* RELATIONSHIP

The fluctuations of bacteria and *Urceolaria* for Vaynol pond, adjusted according to the method outlined above, are compared in Fig. 2. The corresponding graph for College pond is similar. The correlation coefficients are listed in Table 9. The values of r for the bacteria–*Urceolaria* relationship are significant for both ponds; so are the partial

Table 9. *Correlation coefficients for the* Urceolaria *relationships*

	Vaynol pond			College pond		
		Eliminated			Eliminated	
Relationship		Temp.	Bact.		Temp.	Bact.
Bacteria-*Urceolaria*	0·522***	0·522***	—	0·365**	0·290*	—
Urceolaria-temperature	−0·018	—	−0·031	0·659***	—	0·634***

correlations in which the temperature influence is eliminated. In determining r for Vaynol, the treatment of the high bacterial count of 24 January 1949 (p. 69) had to be considered. If seepage of sewage had occurred, unfavourable conditions for *Urceolaria* may have developed despite the increased food supply available, particularly a severe reduction in dissolved oxygen. It was considered safer to omit data for a period long enough to permit the re-establishment of normal conditions, and

a period of three weeks was allowed. The value of r recorded above is based on this compromise. Actually, if only the single sample is omitted, r still has the same degree of significance. The validity of these correlations is again complicated by serial correlation (Moran 1949, 1952) because for both sets of data, the serial correlation coefficients are highly significant. A check on validity has been obtained by using departures from a moving average of five observations to eliminate seasonal trends. On this basis r has a value of 0·359** for Vaynol pond which suggests that the correlation is valid. However, the corresponding value for College pond is $r = 0{\cdot}182$

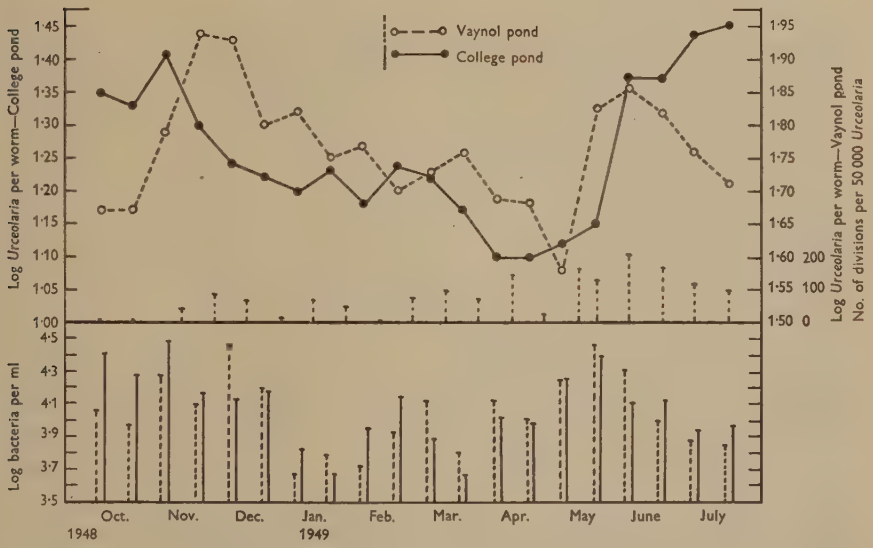

Fig. 3. The fluctuations of *Urceolaria* and bacteria in the two ponds. The number of *Urceolaria* undergoing binary fission is shown for Vaynol pond.

which is not significant. The graph for this pond shows that there is one outstanding period of divergence between bacteria and *Urceolaria* during May 1949. In this period the bacteria increased sharply without an increase in the epizoite. It is probable that the relatively low population of *Urceolaria* resulted from competition with vorticellid peritrichs which reached a peak in the late spring in College pond and occurred in the water samples. The failure of the urceolarian population to increase at this time despite considerable reproductive activity (unpublished data, 1947) also suggests lack of food. The significant negative correlation between host size and the epizoic population in April 1947 (Reynoldson 1950), although not fully understood, also indicates that this is a special period. If the May samples are omitted the value of r (moving average) becomes 0·415** which is significant.

The synchrony of the urceolarian fluctuations in the ponds has also been examined. Since both populations are linked via bacteria to the same rainfall pattern some degree of synchrony might be expected. Alternatively, since they belong to separate

communities an individual community pattern may develop. Comparison of the two populations (Fig. 3) shows that there is particularly close agreement over the period December 1948 to June 1949, with pronounced divergences at either end. The correlation coefficient calculated on a fortnightly basis has a value over the whole period of 0·291 and is not significant, but over the 27 weeks December 1948 to June 1949 the correlation is highly significant ($r = 0{\cdot}681^{***}$).

THE FOOD OF *URCEOLARIA MITRA*

(*a*) *Direct observations on feeding*

According to Sandon (1932) the presence of vestibule, pharynx, etc. is insufficient evidence of the kind of food taken. Since *Urceolaria* is host-specific and can only live a few hours apart from its host its feeding was carefully observed. Examination of *Urceolaria* immediately after removal from its host showed what appeared to be undoubted food vacuoles in the cytoplasm. Later, diatoms were also identified within the peritrich. The ability to ingest particles suspended in water was also proved by placing infested flatworms in a suspension of indian ink, powdered carmine and a colloidal suspension of graphite. Within 10 min black and red 'food' vacuoles, similar in size to those formed under natural conditions, appeared in the protoplasm. After approximately 30 min in these suspensions, ingestion ceased.

Wallengren (1897) has given detailed accounts of the vestibule, pharynx and associated structures in *Urceolaria mitra*. In general they resemble the mechanism found in *Vorticella* and other peritrichs. When apparently feeding *Urceolaria* tends to be elongated in the adoral-aboral plane (Reynoldson 1950) and the adoral cilia stand out stiffly at an angle and do not beat (Fig. 4). The aboral cilia may show some slight activity. The vestibular cilia beat vigorously however. The majority of individuals cluster around the head end of the flatworm, particularly in the region behind the ciliated pits (Fig. 4*b*). Here they 'stand' in the main water currents produced by their host. Observation using ink shows that these currents bring particles within the oral groove of *Urceolaria*. From here the particles are swept into the vestibule by the activity of the vestibular cilia. Subsequent ingestion and evacuation agree substantially with the accounts by Greenwood (1894) and Sugden and Lloyd (1950) for *Carchesium*. It seems clear that *Urceolaria* utilizes the ciliary current of the host for feeding purposes and thereby conserves a great deal of energy compared with free-living peritrichs which have to produce their own feeding current. It is interesting to note that in *Trichodina pediculus* epizoic on *Hydra*, Clark (1866) refers to the adoral cilia as a 'vibratory crown' and 'purveyors of food'. *Hydra* of course has no current-producing apparatus.

(*b*) *Attempts to culture* Urceolaria *under controlled conditions*

Attempts were made to obtain sterile cultures of *Urceolaria* on its host to study the feeding of the peritrich on selected species of bacteria. Despite several washings in sterile water and treatment with *p*-aminobenzene sulphonamide (saturated solution at 15–20° C) followed by streptomycin (0·04% sol.) extending over three days, no real success was obtained. Failure to achieve sterility was due probably to contamina-

tion by material voided by the flatworms. Better results might be achieved by rearing worms from cocoons under sterile conditions and adding *Urceolaria*. However, rapid growth occurred in these experiments and direct examination of the water showed that only bacteria were present, indicating that the epizoite was capable of growing on this type of food alone.

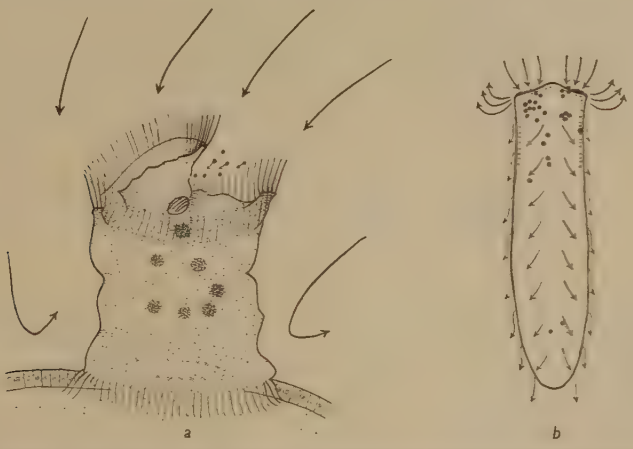

Fig. 4. (*a*) Feeding in *Urceolaria*: the epizoite is shown *in situ* on the host with ink particles about to enter the gullet and a food vacuole forming. Large arrows indicate host-induced water currents. (*b*) The location of an urceolarian population of thirty-one individuals upon their host. Host-induced water currents are also shown, strength of current being approximately proportional to thickness of arrow.

(*c*) *Direct observation of food vacuoles*

The best evidence on the food of *Urceolaria mitra* was obtained by direct observation of the contents of food vacuoles formed under natural conditions. Weekly samples of infested flatworms were collected from Vaynol pond over eight weeks and from College pond over six weeks during April and May 1952. Ten randomly selected *Urceolaria* from each sample were examined with phase-contrast illumination and the number of food vacuoles present was counted and their contents noted. This examination was made within 10–20 min of collecting. The food vacuoles were divided into three main categories on the basis of content: those in which only bacteria were observed, those in which only algae were observed, and those with a mixture of contents including small flagellates. The contents of the last were also mainly bacterial, but some were seen with a majority of pigmented flagellates or green algae. Only very few were seen to contain flagellates of 5–10μ length. These three types of food vacuole were all of approximately the same size, 10–15μ in diameter. The main problem was to be certain of the identification of bacteria, but it was possible in many instances to see clearly the characteristic rod shape and to compare size and appearance with plate-grown, common freshwater bacteria from the same habitat. The appearance of these supposed bacterial food vacuoles also closely resembled the photographs of definite bacterial food vacuoles in Ray's (1951) paper. As a final check, Miss V. G. Collins, of the Freshwater Biological Association has kindly examined *Urceolaria*

from Vaynol, despatched in Vaynol pond water. She reported that the food vacuoles contained mainly short rod bacteria typical of freshwater species.

No attempt has been made to ascertain the relative food values of bacteria, flagellates and algae; the conclusions are based on the quantitative aspect. From an examination of 1286 food vacuoles of Vaynol specimens it is evident that bacteria formed the greater part of the food, 72·2% on average (Table 10). This figure is a minimum because in mixed vacuoles bacteria predominated. This proportion remained fairly constant from week to week except on 23 April when it fell to 42·3%. The algal food vacuoles

Table 10. *An examination of the food vacuoles of* Urceolaria *formed under natural conditions*

	Urceolaria examined	Total food vacuoles	Percentage of each type: Bacterial	Algal	Mixed
		VAYNOL POND			
1952					
2 Apr.	4	43	72·1	27·9	0
9 Apr.	9	221	85·5	12·2	2·3
16 Apr.	10	121	72·7	26·4	0·9
23 Apr.	10	78	42·3	52·6	5·1
30 Apr.	9	158	71·5	20·3	8·2
7 May	10	251	65·3	9·2	25·5
19 May	10	130	65·4	3·1	31·5
26 May	10	284	79·2	1·1	18·7
Total	72	1286 Av.	72·2	13·5	14·3
		COLLEGE POND			
1952					
7 Apr.	10	175	78·9	20·6	0·5
15 Apr.	10	67	55·2	23·9	20·9
22 Apr.	10	59	10·2	79·7	10·2
29 Apr.	7	57	36·8	43·9	19·3
6 May	10	124	14·5	8·9	76·6
22 May	9	82	9·8	1·2	89·0
Total	56	564 Av.	40·4	24·1	35·5

formed only 13·5% on average, but the proportion varied a great deal from week to week. Some of these vacuoles were made up of numbers of small green cells, a few of single large rounded cells while there were also numbers of individual diatoms about 10μ in length of a *Nitzschia*-like type. There is little doubt that *Urceolaria* is able to digest these diatoms because all stages have been seen from individuals with a large chloroplast to the empty valves. A rather different picture was shown by the 564 food vacuoles from College pond specimens. In these, although the bacterial type of food vacuole formed a majority they amounted to only 40·4% of the total. It appeared that these *Urceolaria* fed relatively more on algae and perhaps flagellates. However, the 40% value is probably much below actuality because the mixed vacuoles, predominantly bacterial, formed 35·5% of the total. The difference between the two ponds, however, seems quite distinct on a qualitative basis.

The evidence also suggests that the number of food vacuoles formed per *Urceolaria* was different in the two ponds. In College pond 10·1 food vacuoles were recorded, for Vaynol pond 17·9, an increase of nearly 80%. There also seemed to be a com-

parable dissimilarity in purely bacterial food vacuoles. Such a difference in feeding rate would account in part for the difference in size of the two *Urceolaria* populations. But how this can occur in the presence of an apparently similar bacterial population in each pond is not understood. An undetected disparity between the two bacterial populations due to coliform organisms seemed unlikely because they usually form such a small proportion of the total. However, to check this point samples were taken in 1953 during wet and dry periods, and plated at 37° C (using MacConkey's medium) as well as at 20° C. The presumptive coliform count was of the order of 100–2000 per ml and there was no real difference between the two ponds. This cannot therefore explain the different feeding rates.

OTHER FACTORS AFFECTING THE BACTERIA–*URCEOLARIA* RELATIONSHIP

(*a*) *The role of flagellates*

Correlation between bacteria and *Urceolaria* could be regarded as symptomatic only, some other factor or factors being causative. Of these, an alternative source of food, particularly small flagellates, seemed most likely. Direct utilization of dissolved organic materials is also possible but seems remote as an important factor because of the adaptations of *Urceolaria* for particulate feeding. Additionally, such feeding in ciliates occurs in simply organized types apart from *Paramoecium* (Lwoff 1951), and in this case it does not necessarily mean that the mechanism is important in nature. The latest work (Evans & Pendleton 1952) with *Paramoecium* using radio-active tracers suggests that uptake of dissolved materials is slight compared with particulate feeding.

Direct counts of flagellates were made using the technique of Cole & Knight-Jones (1949), together with estimates of bacteria by plating and counts of *Urceolaria*. Only flagellates $\leqslant 10\mu$ in length were included since these seemed to be near the upper limit of food size of *Urceolaria*. The majority of the flagellates observed were between 3 and 5μ in length. The results for a ten-week period of observation are recorded in Table 11. At the beginning the *Urceolaria* population was at a very low level, 29·5 per worm, and throughout the ten weeks it increased continuously to reach the highest level ever recorded in this work, 172·5 per worm. If the bacterial trend is compared it is clear that except for the initial period there is good agreement. However, at a low population level the factor limiting increase is probably maximum feeding rate rather than amount of food available, and in the initial stages of the period the bacterial data should be compared with percentage increase (Table 11, last column) and not with the average population. Thus the temporary low level of bacteria on 2 April, following a dry period, seems to be reflected in a reduction of growth-rate. There is also substantial agreement between the flagellate and urceolarian fluctuations, and both relationships have a significant correlation coefficient ($P < 0{\cdot}001$). Nevertheless, during the five weeks from 2 April when both bacteria and *Urceolaria* were increasing steadily, the flagellates remained stationary; on balance the bacteria–*Urceolaria* agreement is the more convincing. This view is strongly supported by the evidence from the food vacuoles and indicates that flagellates are less important than bacteria in

determining the population level of *Urceolaria*. It should be remembered that in comparing abundance of flagellates and bacteria the former is a direct count. Determining bacteria in this way on two occasions gave values from six to nine times larger than the plate count. Although it is difficult to allocate border-line organisms (Gross, Raymont, Nutman and Gauld 1946, Knight-Jones & Walne 1951) unquestionably bacteria were much more numerous than flagellates.

Table 11. *Competition and alternative food sources*

The data for the *Urceolaria* population are set back by one week.

	Planktonic ciliates per l.	Protozoa per mm² of substratum		Flagellates ($\leqslant 10\mu$) per ml	Bacteria (plate) per ml	*Urceolaria* per worm one week later	Increase	
		Total	Vorticellidae				Absolute	%
1952	—	—	—	—	—	29·5		
19 Mar.	—	—	—	20000	53000	45·7	16·2	54·9
26 Mar.	150	—	—	70000	21500	55·7	10·0	21·9
2 Apr.	150	60	0	80000	6300	64·0	8·3	14·9
9 Apr.	0	32·5	7·5	50000	17100	69·8	5·8	9·1
16 Apr.	10	17·5	10·0	64000	14700	78·7	8·9	12·8
23 Apr.	0	—	—	50700	23000	86·9	8·2	10·4
30 Apr.	50	17·5	5·0	64000	54400	93·0	6·1	7·0
7 May	100	—	—	156000	151000	147·0	54·0	58·1
19 May	300	17·5	5·0	179000	183000	159·8	12·8	8·7
26 May	2230	15·0	5·0	86000	147500	—		

(*b*) *The influence of predators, parasites and competitors*

Apart from food supply the other important factors which may regulate a population are predators, parasites and competitors. It is quite certain that predators have played no part in determining fluctuations of the urceolarian population. Of the many thousands of flatworms examined no possible predator of *Urceolaria* has been seen. Goodrich (1938) reported that *Urnula epistylides*, a suctorian, feeds on epizoic peritrichs such as *Zoothamnium*, *Carchesium* and *Epistylis*, but no evidence for a similar predator of *Urceolaria* exists. The problem of parasites is not so easily dismissed. Padnos & Nigrelli (1947) reported a suctorian, *Endosphaera engelmanni*, as an endoparasite of *Trichodina spheroidesi*. In earlier work considerable numbers of *Urceolaria* were stained in methylene blue and examined under the microscope. *Endosphaera* or a comparable genus was not observed. The possibility of virus or bacterial diseases cannot be ruled out entirely but the urceolarian populations in neither pond showed cataclysmic declines which are often associated with parasitic regulation.

A limited study of competition has been made mainly from the viewpoint of competition for food. It is quite apparent that a suitable substratum, often a limiting factor for sessile organisms, was not operative particularly in the case of the College pond population. Even with the maximum average population for Vaynol of 93·2 *Urceolaria* per worm, it has been calculated that for a medium-sized worm of 7·0 mm length, less than one-quarter of the dorsal surface would be covered. If the highest population recorded for an individual worm (275) is considered, there is still a third of the substratum unused. It does not follow that every part of the worm is equally suitable, but provided food is adequate the epizoite could cover the entire dorsal

surface of the worm. This view was confirmed in collections of *Polycelis felina* (Dalyell) from a stream near Bangor during 1953 which showed the dorsal surface entirely covered by *Urceolaria*.

In considering competition for food attention has been concentrated on other species of Protozoa, particularly peritrichous forms. Correlation between bacteria and *Urceolaria* seemed equally strong winter and summer alike, particularly for the Vaynol population, and therefore any potential competitor with a marked seasonal periodicity such as small planktonic crustacea seems to be excluded. It was intended to study the spring–early summer period in College pond for which there was evidence of competition (p. 71). The drastic reduction of *Polycelis tenuis* prevented this and Vaynol conditions had to be observed instead.

It is becoming evident that freshwater Protozoa are divided fairly sharply into two or perhaps three broad ecological categories (Picken 1937). Those which are planktonic, those free-living forms which live close to the substratum and the sessile forms. For the present purpose the two latter groups may be considered together. The number of planktonic forms per unit volume was estimated by using the method described for counting marine flagellates (Cole & Knight-Jones 1949). The substratum population was estimated by counting areas on slides which had been immersed in the pond. In the first method, two samples of pond water were taken each week as for bacterial counts, over nine weeks from 26 March to 26 May 1952. Two 50 ml subsamples from each sample were concentrated by filtration to 1 ml and one-tenth examined under the microscope; also in most cases the whole concentrate was examined. The number of Protozoa of approximately 20μ length and upward were estimated per litre. In the slide method, glass slides held in a wooden frame were left in the pond for two weeks and then the Protozoa on twenty areas each of 1 mm^2 were counted on each of two slides. Records of the *Urceolaria* population and the bacterial and flagellate populations were also kept. The data are summarized in Table 11. The population of planktonic Protozoa remained low over the greater part of the two months but in the last two weeks a large population of *Halteria grandinella* developed. This species is recorded as a bacterial feeder (Sandon 1932) and at a concentration of 2230 per litre was probably competing with *Urceolaria* for food although there was no evidence that the *Urceolaria* population was adversely affected at this time. But an effect may have become evident later, after sampling had ceased. In view of the rapid fluctuations of bacteria initiated by rainfall it is improbable that the small population of planktonic Protozoa up to 150 per litre would exert a decisive influence. Thus although the data are not extensive they show that long periods occur when competition is unimportant; the overall picture suggests that it does not occur extensively.

After a fortnight's immersion the slides were coated with a 'jungle' of filamentous algae and diatoms with rotifers, gastrotrichs and various Protozoa moving among the filaments. In no case was the same species of Protozoa recorded both in the plankton and from the slides. It was also noted that when such slides are placed in a vessel (in water) substratum forms remain associated with the algal covering. The existence of such a sharp demarcation was also supported by the absence of substratum species from samples of water taken 2–3 mm above decaying leaves in the pond. The following fauna was recorded from the slides, 'plus' signs indicating relative abundance: *Amoeba*,

Colpidium (+), *Euplotes*, *Glaucoma*, *Lionotus* (++), *Loxodes* (+++), *Oxytricha* (+), *Pleuronema* (+++), *Stylonichia*, *Tachysoma*, *Trichoda*, *Vorticella* (+++), *Zoothamnium*. The quantitative data are recorded in Table 11. A point which arises is whether or not *Urceolaria* is likely to compete with the free-living substratum species. Measurements show that the adoral surface of *Urceolaria* is raised approximately 1·0–1·5 mm above the substratum depending upon the size of the flatworm. A total of twenty-six measurements of the maximum thickness of the algal mat made from ten slides during the period of observation showed a range of 1·03–0·15 mm with an average of 0·57 mm. This suggests that *Urceolaria* draws its food from a different niche to that of unattached ciliates. The latter seem to feed within the mat mainly on algae and perhaps sessile bacteria. The stalked ciliates, however, are probably capable of reaching the feeding zone of *Urceolaria* and competition might be expected from them. Food vacuoles of *Zoothamnium* seemed to have similar contents to those of *Urceolaria*. The food vacuoles of *Vorticella* tended to contain more green algae but as twenty only were examined this may be a chance result. The sessile peritrichs reached a maximum number of 10·0/mm² and at this concentration did not exert a detectable influence on the increasing *Urceolaria* population (Table 11).

DISCUSSION

Before considering the more general aspects of this population study, there are two types of apparent anomaly to be examined. The first concerns differences in interaction between the organisms and their physical environment in Vaynol and College ponds over the same period of time; the second relates to differences between the 1946–47 and 1948–49 results for College pond. The former is apparent by a comparison of the partial correlation coefficients for the rainfall–bacteria and temperature–bacteria relationships in the two ponds; for College pond these are 0·370** and 0·295*, for Vaynol 0·456*** and 0·091 respectively. Thus whereas the College pond data show correlation of bacteria with both rainfall and temperature, the Vaynol data show only strong correlation with rainfall. Fig. 3 shows that this difference is due mainly to the high bacterial population in College pond during October 1948, a relatively warm month. No explanation can be offered to account for this. Comparing the two urceolarian populations, there is an even greater contrast in apparent reaction to temperature as shown by partial correlations of 0·634*** for College pond and −0·031 for Vaynol. This can in part be explained by the above difference in bacteria, but not entirely. During June and July the population trends of *Urceolaria* were different in the two ponds despite the general similarity in the bacterial populations (Fig. 3). The College population showed an upward trend which paralleled temperature while the Vaynol population showed a decline which paralleled bacteria. The bacterial population in College pond showed the lesser decline but this cannot account for the difference in behaviour of the *Urceolaria* populations. There is evidence that College pond *Urceolaria* feed to a relatively greater extent on planktonic algae (p. 74). If the algal population remained high it might prevent a reduction in *Urceolaria* following a decline in bacteria. No data for the algal population at this period are available, but on general grounds large numbers would be expected during May,

June and early July. In support of this argument we have the high *Urceolaria* populations in June and July 1947 (Reynoldson 1950) which accompanied low rainfall and therefore presumably, low bacterial numbers. Such an explanation would also account for the lower strength of the correlation between bacteria and *Urceolaria* in College pond. Later in the summer College pond is extensively covered with a growth of duckweed (*Lemna* sp.) which curtails the growth of green algae.

Turning now to the second anomaly, in the 1946–47 work the partial correlation coefficient for the *Urceolaria*-temperature relationship was 0·164 compared with 0·634*** for the 1948–49 period, the former being more in line with the Vaynol result. This contrast can be explained by a difference in the incidence of the rainfall in the two periods. A concise summary of this is given by the correlation coefficient for rainfall-temperature. Based on the 1946–47 data it is −0·880***, i.e. most of the rain fell in the cold weather; for 1948–49 it is −0·133, i.e. much less rain fell in the cold weather. It has been pointed out (Reynoldson 1950) that if rainfall and temperature tended to 'pull' together, then a positive correlation with temperature as well as rainfall would result. This seems to have happened in 1948–49 and accounts for the contrast in the two years. The difference in the incidence of rainfall is brought out clearly in Table 12. It follows also that during a particularly wet summer positive correlation between temperature and *Urceolaria* is probable for Vaynol conditions but adequate food would always be a primary necessity and therefore adequate rainfall. Temperature is a secondary factor.

Table 12. *Rainfall during 1946–47 and 1948–49*

		Average monthly rainfall (in.)			
		Absolute		Percentage	
	Temperature (° F)	1946–7	1948–9	1946–7	1948–9
Jan., Feb., Mar., Nov., Dec.	<45	5·66	3·17	49	36
Apr., May, Oct.	45–55	3·50	3·09	30	35
June, July, Aug., Sept.	>55	2·44	2·61	21	29

A further contrast marked the results of the two periods in College pond. The average number of *Urceolaria* per worm for 1946–47 was 22·7 (S.D. ± 16·439), for 1948–49 it was only 10·2 (S.D. ± 8·420). The means differ significantly with $t = 20{\cdot}57$ ($P < 0{\cdot}001$). If the thesis that the abundance of *Urceolaria* is determined mainly by the abundance of bacteria is correct then a higher bacterial population in 1946–47 would be expected. Lacking data for bacteria for both periods the rainfall has been compared. The average monthly rainfall in 1946–47 was 4·06 in. while in 1948–49 it was only 2·96 in., i.e. a much higher bacterial population in 1946–47 would result. It would also follow that the Vaynol population of *Urceolaria* during 1948–49 was relatively low and it is interesting to note the particularly high populations during May 1952 for Vaynol which accompanied heavy rainfall and high bacterial populations (Table 11). The rainfall over the relevant period was 0·58 in. in 1948–49 and 1·87 in. in 1952.

Changes in birth- and death-rates are ultimately responsible for population

fluctuations. Data for birth-rates are usually easier to demonstrate and it is instructive to compare phases of reproductive activity (binary fission) in *Urceolaria* with population changes. There are two major peaks in the *Urceolaria* population—Nov.–Dec. 1948 and May–June, 1949. These coincide well with the two best defined cycles of binary fission. During the intervening period there are two minor cycles of recovery by *Urceolaria* and each is associated with an increased tempo of division. Thus in a general way reproductive activity seems to be paralleled by an increase in the population. There is one clear exception, however, the high reproductive activity in April was associated rather with a decline, and in view of other evidence (p. 71), seems to be an effect of competition, although no proof of this could be obtained in the 1952 observations. The ratio of the number of individuals undergoing binary fission to total population varies considerably during the annual cycle. It is particularly high during the summer without however producing a large population, indicating that although the population growth-rate is high at this time it is matched by a high mortality-rate. The latter may result from food shortage, but it is puzzling that this should be accompanied by a high reproductive rate unless rate is stimulated by some seasonal abiotic factor such as temperature. A better understanding of the stimuli affecting binary fission is needed.

Gray (1951*a*, 1952), studying the microbiology of a stream, demonstrated the effect of rain and drought on bacteria. He found no relationship between the total bacteria and total ciliate populations. But his results are complicated by the washing in of soil Protozoa, and it also appears that he was dealing mainly with Protozoa on the substratum while bacteria were sampled in the open water. There was, however, significant correlation between Gram-negative bacteria and ciliates. Although some Protozoa are selective feeders or may thrive better on certain bacterial types (Calkins & Summers 1941, Singh 1946) in view of the catholic feeding of *Urceolaria* it is unlikely that a higher degree of correlation would have been found by comparison with particular bacterial strains. Gray (1951*b*) also provided evidence of a lunar periodicity for *Stylonichia mytilus*; Mr M. J. R. Healy has kindly analysed the 1946–47 data from this aspect, and it is definite that no such periodicity occurred for *Urceolaria*.

The factors responsible for the clear-cut difference in average density of *Urceolaria* in the two ponds have not been studied except to show that host density is not involved. As Solomon (1949) has pointed out, it is not only impossible but illogical to separate absolutely the determinants of population fluctuations and density, but experience suggests that the latter is determined rather by all the chief elements of the ecosystem (for references see Solomon 1949). The ponds described here differed markedly in the chemical properties of the water (p. 59) and the amount of light reaching them. To what extent such factors were responsible for the density of *Urceolaria* is not known.

Correlation, which has been used extensively in this paper, may be interpreted in one of three ways. It may describe a spurious relationship, it may be due to direct causation, or it may result from both variables being influenced by a common factor. The basis of correlation between rainfall and bacteria is complex and not sufficiently understood for profitable discussion. Neither does it follow that conclusions reached for lakes are applicable to ponds; although Taylor (1949) has shown for lakes that

washing in of soil bacteria is an unimportant contribution, this may not be so for ponds. There is much evidence that the bacteria–*Urceolaria* relationship results from direct causation, bacteria forming the main food of *Urceolaria*. Limited divergences seem to be attributable to competition and in College pond to an alternative summer food source. There is no indication that *Urceolaria* exerts a regulatory influence on the bacterial population such as seems to occur in soil organisms (Cutler, Crump & Sandon 1923). Indeed, considering the small numbers of *Urceolaria* in relation to water volume and also the rapid changes in bacteria, such an effect would be surprising. The other principal factors which may determine population fluctuations are predators, parasites and competitors. The first are definitely inoperative here, and no evidence was found to suggest that parasites were important. Evidence for interspecific competition was circumstantial only, but was derived from several sources (p. 71), suggesting that competition for food with peritrichous ciliates lowered the urceolarian populations during April–May. Biotic factors of this type seem to exert a limited influence. Of the climatic factors, temperature, usually the most important influence on invertebrate populations in temperate regions, is relegated to the background. This occurs because it can only act as an accelerator of growth in the presence of sufficient food. In our climate since rain falls mainly in the colder months the food supply is not adequate. It follows that the influence of temperature varies from year to year and from one locality to another depending on the incidence of rain.

The ultimate object of this work is to discover the factors which 'regulate' the population and in particular to decide whether their operation is density-dependent or not. The present trend of thought on this subject among many British ecologists is to regard only density-dependent control as important (e.g. Varley 1952, Elton & Miller 1954). With our present meagre knowledge of field events this seems to be unjustified. In the present case a decision cannot be reached until conditions *within* individual host populations have been studied. Work on this is proceeding.

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SUMMARY

1. The basis of the previously established relationship between rainfall and fluctuations in the population of *Urceolaria mitra* Von Sieb epizoic on the freshwater triclad *Polycelis tenuis* Ijima has been examined.

2. Observations were made on two ponds and their abiotic and biotic characteristics compared.

3. The epizoic populations of individual worms were not influenced by changes in the host population.

4. Weekly samples over one year showed that fluctuations in the bacterial population were largely determined by rainfall, the variations in each pond showing a high degree of synchronization. The rainfall pattern impresses itself clearly on the bacterial population because the effect is short-lived—three to four days.

5. When adjusted for a time lag the fluctuations in bacteria and *Urceolaria* were significantly correlated for both ponds. This explains the rainfall–*Urceolaria* connexion. The two *Urceolaria* populations showed synchrony during most of the year; minor contrasts were attributed to differences in food supply.

6. The feeding method and food of *Urceolaria* were studied experimentally and by examination of naturally formed food vacuoles. In the ponds it fed mainly on bacteria but also on flagellates, green algae and diatoms. Attempts to obtain sterile cultures were largely unsuccessful but it was demonstrated that the peritrich can grow on bacterial food alone.

7. No predators or parasites of *Urceolaria* have been observed. Competition for food by peritrichs may have reduced the urceolarian population for a short time in the late spring.

8. Changes in the small flagellate population (a possible alternative food), bacteria and *Urceolaria* were followed for ten weeks. Closer agreement was found between bacteria and *Urceolaria* than between flagellates and *Urceolaria*.

9. Phases of reproductive activity in *Urceolaria* generally produced an increase in the population.

10. It is concluded that fluctuations in *Urceolaria* are largely initiated by changes in the bacterial population which in turn are due to rainfall. Temperature is a secondary factor only.

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* Quoted only at second hand.

STUDIES ON A POPULATION OF *DAPHNIA MAGNA*

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(With 7 Figures in the Text)

In May 1952 Dr F. Greenshields of the London Metropolitan Water Board informed the Zoology Department of Bedford College about the presence of vast numbers of *Daphnia magna* Straus in a sludge settling tank at Hampton Water Works. The animals were bright red with haemoglobin in the blood and were present in such numbers that large patches of the water surface were streaked red as if with blood. A fortnight later the animals were coated with a layer of the stalked euglenoid, *Colacium vesiculosum* Ehrenberg (kindly determined by Dr E. G. Pringsheim), which masked the red colour of the blood and gave the animals a green appearance, while the motile forms of the euglenoid coloured the surrounding water bright green (cf. Green 1956). The females of *Daphnia magna* were producing very few parthenogenetic eggs at that time. Berg (1931) has shown that in Endrup Dam, Denmark, the population of *D. magna* shows a great drop in parthenogenetic egg production in May, followed by a period of sexual reproduction. As it was thought that a similar phenomenon might have occurred at Hampton it was decided to follow the population in one of the settling tanks from April to July in 1953. Preliminary samples were taken in June, October, November and December 1952, and one sample in March 1953. From 17 April 1953 onwards samples were taken at approximately weekly intervals up to 10 July when the last one was taken. During the late summer the settling tank became so full of sludge that the population of *D. magna* died out.

METHODS

Samples were collected by Mr J. Baker of the Metropolitan Water Board, using a net which would allow very small animals to pass through: in this way only the adult population was sampled, and the large number of copepods which were normally present were allowed to escape. The samples were transported to London and examined on the same day. No attempt was made to evaluate any of the physical and chemical factors in the water: any such attempt would have been most difficult to interpret because the settling tanks are frequently receiving fresh supplies of water heavily laden with dead and living animals from the filter beds. The composition and density of the suspended matter fed into the settling tanks would in turn depend upon the conditions in the reservoir from which the water was drawn. The present investigation was limited to a study of variations in the composition of the adult population and variations in size, egg production, haemoglobin content of the animals, and the density of epibionts on the carapace.

The percentage composition of the population was estimated by taking random samples from the main sample with a wide pipette and ejecting them on to a glass

plate, then draining off most of the water and examining under a low-power binocular microscope. In this way a sample of at least a hundred individuals was examined, and generally about 300. The categories into which the specimens were grouped were:

(1) Females with parthenogenetic eggs or embryos in the brood pouch or with large ovaries indicating that egg laying was imminent.
(2) Females of mature size (over 2·5 mm long) without eggs or large ovaries.
(3) Females with ephippia.
(4) Immature females between 1·2 and 2·5 mm long.
(5) Males.

Very small animals under about 1·2 mm long, in their first or second instar, were ignored.

When estimating length, haemoglobin content, egg production and epibiont populations, samples of twenty females with parthenogenetic eggs or embryos in the brood-pouch were used. The length of each animal from the crown of the head to the base of the tail spine was measured with an eyepiece micrometer. The haemoglobin content was estimated by the index method of Fox (1948); the index obtained by this method was then corrected by dividing it by the mean length of the animals in the sample, and then multiplying by three. This correction is necessary because the uncorrected index is obtained by looking through the depth of the animal at the base of the antenna and so is a combination of concentration and depth. The depth of the animal in this region is directly proportional to the length of the animal (Green, unpublished results). All the corrected indices are thus given in terms of concentration at a length of 3 mm. The haemoglobin index for a sample of twenty males, when present, was corrected in the same manner.

Egg numbers were counted after dissecting the eggs out of each animal under a low-power binocular microscope.

The numbers of *Colacium vesiculosum* were estimated by viewing the animal under a 16 mm objective and a × 10 eyepiece and counting the number of cells of *Colacium* in a square with sides of 0·13 mm (= 10 divisions on the eyepiece micrometer) located at a distance of 0·9 mm from the base of the tail spine (Fig. 1). When there were no cells of *Colacium* in the area, or anywhere else on the animal, the value was recorded as 0. When *Colacium* was present elsewhere on the body but not in the square the value was recorded as 1. If one cell was in the square as well as others being present elsewhere the value was recorded as 2. Values above this were obtained by counting the cells in the square and adding 1. The mean value obtained from the sample is here termed the *Colacium* index. It would of course have been more satisfactory to have counted all the cells of *Colacium* on each animal, but when *Colacium* is even moderately abundant the numbers present would be impossible to count in a reasonable time—the number on an animal 2·5 mm long with an index of 20 would be somewhere in the region of 9000.

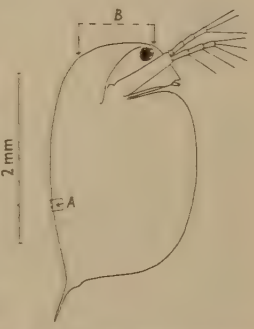

Fig. 1. *Daphnia magna* female; lateral view to show regions used in estimating the density of epibiotic populations. A, area in which *Colacium vesiculosum* was counted, B, limits between which peritrich ciliates were counted.

The numbers of peritrich ciliates were estimated by a similar method, but in this case the number attached to the crown of the head between the limits shown in Fig. 1 was counted. Again the value of 1 was recorded when peritrichs were elsewhere on the body and not in the estimating region. The two regions used for estimating the frequency of these epibionts were chosen because they were found by experience to be the most frequently settled areas when moderate populations of the epibionts were present. Rotifers (*Brachionus rubens* Ehrenberg) were estimated by counting the total number attached to each female *Daphnia magna*.

On some occasions the epibionts were very sparse and a larger sample had to be taken in order to estimate the index. In this case a random sample of a hundred hosts was examined.

POPULATION DENSITY AND COMPOSITION

The data obtained in 1952 are summarized in Table 1 and Fig. 2. They will not be discussed in detail as most of the phenomena are similar to those examined in greater detail in 1953. The main features of note are the similar fluctuations in mean length and egg number, and the inverse relation between haemoglobin content and egg

Table 1. Daphnia magna *at Hampton, summer 1952*

	Population composition			Females with parthenogenetic eggs					
	% females with eggs	% females ephippial	% males	Mean length (mm)	Mean egg number	Haemoglobin content	*Colacium* index	Peritrich index	Rotifer index
15 May	14	1	32	2·99	4·4	106	7·1	10·0	0
19 May	60	4	7	2·82	3·7	123	22·6	11·0	0
29 May	88	0	0	3·10	7·5	86	60·0	14·0	1
11 June	56	0	0·5	3·74	19·0	59	12·5	21·3	48·6

number. Of the epibionts *Colacium* showed a great drop in index which coincided with an increase of the rotifer *Brachionus rubens*. It is possible that the increase of this rotifer was to some extent responsible for the drop in the *Colacium* index, since the motile stage of *Colacium* was seen to be ingested by the rotifer. The 1953 results indicate that the two phenomena are not necessarily directly related. The peritrichs showed a slow steady increase in index, but there was a change in the specific composition of the population. In the early samples *Rhabdostyla pyriformis* Perty and *Intrastylum invaginatum* Stokes f. *daphniae* Kahl were the most frequent species, but later a species of *Carchesium* became abundant. In the sample taken on 11 June a suctorian, *Acineta* sp., was found in small numbers on the margins of the carapace. The diatoms *Cocconeis placentula* Ehrenberg and *Synedra* sp. were also found attached to the carapace in this sample.

Four samples were examined between 2 October and 5 December (Table 2). On the last date the tank was covered with a layer of ice $\frac{1}{2}$ in. thick. In these samples the population was producing few eggs; the percentage of females with parthenogenetic eggs was low and a mild sexual period was in progress. The haemoglobin content was very low and barely measurable at the beginning and end of this period. Epibionts

were sparse, but an amoeboid parasite, *Pansporella perlexa* Chatton, was present in considerable numbers in the gut of *Daphnia magna*. Estimates were made of the frequency of occurrence of this parasite in animals of different sizes and condition. The technique used was to dissect out the gut and, under a low-power binocular microscope, scrape out the parasites with a needle, then count them using reflected light in which they appear as opaque white objects. Wide variations in the degree of infection were found (Table 3). Large females without eggs had the heaviest infections; possibly the heaviness of the infection was a contributory cause of their inability to

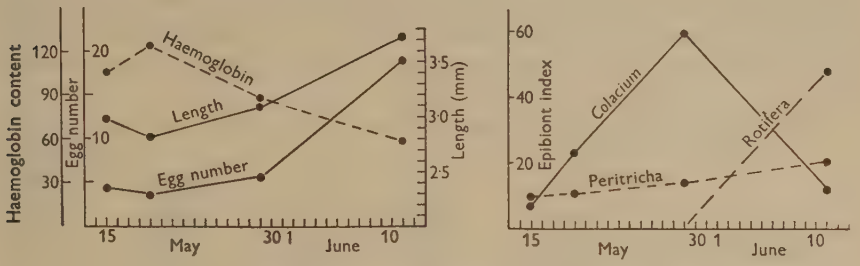

Fig. 2. The *Daphnia magna* population in early summer 1952.

produce eggs. Newly liberated young were the least infected. Females with parthenogenetic eggs and females with ephippia had infections that were heavier than in newly liberated young, but lighter than in eggless adult females. In immature females the degree of infection increased with the size of the host. Mature males and mature females showed no significant difference in degree of infection. During this period another epibiont, not found in the summer, was noted. This was *Amoebidium parasiticum* Cienkowski, which was found mainly on the antennae. The life-cycle and systematic position of this epibiont have recently been investigated by Tuzet & Manier (1951). It is only recently that this epibiont has been recognized in Britain (Johnson 1952).

Table 2. Daphnia magna *at Hampton, winter 1952*

	Population composition			Females with parthenogenetic eggs					
	% females with eggs	% females ephippial	% males	Mean length (mm)	Mean egg number	Haemoglobin content	*Colacium* index	Peritrich index	Rotifer index
2 Oct.	6	10	34	—	3	15	1	1	0
18 Nov.	4	4	6	2·92	3·7	—	0·1	1	0
28 Nov.	4	3	2	—	—	—	—	—	—
5 Dec.	0·5	7	4	2·97	3·5	15	—	—	—

In 1953 it was not possible to make direct estimates of the density of the population since when the tank was first examined it was evident that the distribution was extremely patchy, parts of the surface being densely crowded and other parts very sparsely populated. In the densely crowded areas there would be several thousand specimens of *Daphnia magna* per litre, whereas in the sparsely populated regions there would be less than ten per litre. However, it was possible to make subjective observa-

tions on the population density by noting if 'shoals' were forming at the surface or whether the population appeared to be dispersed, and also by noting how quickly a large sample could be collected. From this sort of information it is possible to say that in March, April and early May the population was dispersed and not crowded. On 12 May the population was densely crowded and was forming shoals at the surface. On 29 May there was a marked reduction in the population; possibly many had died from overcrowding. These fluctuations in density were reflected in the composition of the population. In April and early May the percentage of females with eggs was high, but between 5 and 12 May there was a dramatic drop in this percentage. At the same time males appeared in the sample, but it was not until the next collection (19 May) that females with ephippia appeared. The period of sexual reproduction was

Table 3. *Infection of* Daphnia magna *with* Pansporella perplexa

	Host	Number examined	Mean length (mm)	Mean number *Pansporella* per host	Maximum number in single host
18 Nov. 1952	Males	10	2·01	10·5 ± 2·8*	36
	Mature females	10	2·60	10·9 ± 2·9	35
28 Nov. 1952	Immature females	10	1·64	14·7 ± 1·7	21
	Mature females	10	3·00	27·8 ± 4·0	61
5 Dec. 1953	Immature females				
	a	11	1·15	3·0 ± 1·8	18
	b	8	1·60	14·9 ± 2·2	22
	c	9	2·02	20·0 ± 4·5	43
	Mature females				
	With eggs	11	2·97	16·0 ± 2·2	31
	With ephippia	10	2·90	21·5 ± 3·3	39
	Without eggs	14	2·99	30·8 ± 7·5	114

* Standard error of mean.

short and not very intense. The percentage of females with ephippia dropped to a very low level in the sample taken on 29 May and did not rise above 2·5% in any of the later ones. The density of the population when these later samples were taken never again appeared to be as great as it was on 12 and 19 May, although the density was higher than it was in April, and small shoals were occasionally seen.

The occurrence of sexual reproduction when the population was at its densest is in agreement with the observation of Berg (1931) who found that in several species of *Daphnia* in Denmark ephippial females appeared when the populations were densely crowded.

SIZE AND EGG PRODUCTION

The fluctuations in mean length of the females carrying parthenogenetic eggs are recorded in Fig. 3. In April and early May the females were large, some measuring up to 5·0 mm in length. There was a great drop in mean length between 12 and 19 May; thereafter the fluctuations were small, with the mean length never again reaching its former level. The large drop was due to the deaths of the overwintering females.

MacArthur & Baillie (1929) have shown that the mean length of life in *D. magna*

varies inversely with temperature and that at 8° C the mean length of life for females is 108 days. Since the settling tank was at one time covered with ice it is probable that some of the large females found in early May lived even longer than this and may have been four or five months old before they died. MacArthur & Baillie also showed

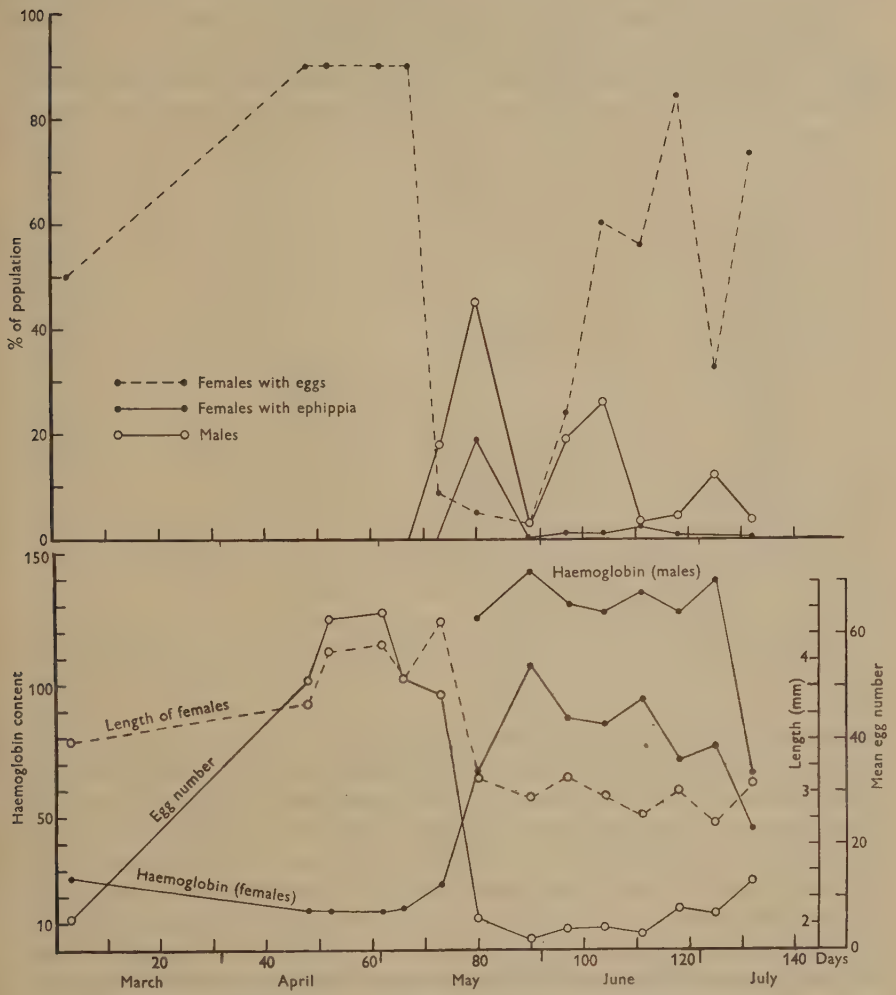

Fig. 3. The *Daphnia magna* population during spring and early summer 1953.

that females grown at 8° C reached a larger final size than others grown at 18 or 28° C. This is in agreement with the finding that in the warmer months of June and July the mean length did not again reach that found in early May, although this may have been due to quite different reasons such as the level of nutrition being lower or the fact that the population was much denser.

When a sample of parthenogenetically reproducing females of *D. magna* is examined there is found to be a positive correlation between size (length) and the number of eggs in the brood pouch (Green 1954). Such a relation is shown for two samples from Hampton in Fig. 4. The number of eggs produced by a female varies with various environmental factors, so that during a period of time widely differing numbers of eggs per brood may be induced by changing conditions. There is, in the samples from Hampton, a striking agreement between the fluctuations in size and the fluctuations in egg production. This is surprising, but may be explained by the fact that the samples were taken at random, and the values for mean length and mean egg

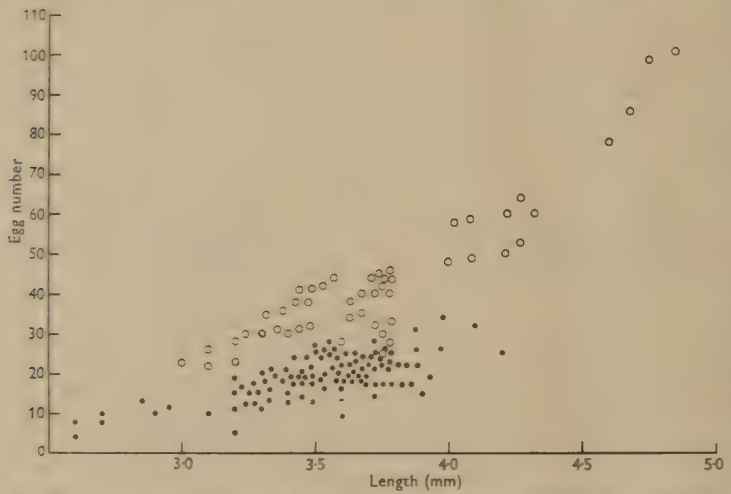

Fig. 4. The relation between length and egg number in female *Daphnia magna* at Hampton. Black dots, 11 June 1952; open circles, 5 May 1953.

number will be affected by the presence of newly mature females in the sample. The length and egg number of these newly mature females will be affected by the conditions under which they have grown, and since conditions which favour growth also favour egg production (cf. Edlén 1943, Green 1954) the two will tend to fluctuate together. The most striking case at Hampton was the considerable drop in egg production when the large overwintering females died, and their numerous offspring matured under very crowded conditions. The fluctuations in egg production per animal followed the fluctuations in the percentage of females carrying eggs. This latter measure of reproductive capacity fluctuated more widely and somewhat in advance of the mean egg number. This again was particularly striking between 5 and 12 May when the percentage of females with eggs dropped from 90 to 9, while the mean egg number only dropped from 51·5 to 48·9. The next sample however showed a drop to a mean egg number of 6·0. The percentage of females carrying eggs in June also rose much more than the mean egg number.

Wide fluctuations in the percentage carrying eggs are to be expected, since if at one time there is a large percentage carrying eggs, then a short while afterwards there

will be a correspondingly large number of young liberated. These young will markedly reduce the percentage with eggs until such time as they become mature. Apart from the mere numerical effect that the liberation of a large number of young would have there may also be crowding effects which would reduce the mean egg number and the percentage carrying eggs.

HAEMOGLOBIN CONTENT

The fluctuations in haemoglobin content are recorded in Table 4 and Fig. 3. The first striking feature is the strong steady increase between 5 and 29 May, when the highest index was recorded. This is the first time that the rate of gain of haemoglobin in a natural population has been studied. The second important feature is the constantly higher haemoglobin index of the males. The rate of gain in males also appears to be more rapid than in females. No males were recorded in the population on 5 May though some may have been present among the very small animals which were ignored; these would not however be much more than four days old. Thus the males which had a haemoglobin index of 126 on 19 May were at most eighteen days old. The rate of loss of haemoglobin from males was also greater than from females (Fig. 3). This is surprising since females pass haemoglobin from the blood into the eggs (Dresel 1948) and this might be expected to increase their rate of loss.

It is noteworthy that the fluctuations in haemoglobin index are inversely related to the fluctuations in mean egg number during the period of observation. It seems, however, that the relationship is not a direct one, for the haemoglobin index of the males fluctuates parallel to that of the females. The explanation seems to be that conditions which favour haemoglobin synthesis are not favourable for egg production. In fact Fox, Gilchrist & Phear (1951) have shown that egg production is directly related to the oxygen content of the surrounding water when other conditions are constant. Fox and his co-workers (Fox 1948; Fox, Hardcastle & Dresel 1949; Fox & Phear 1953) have also shown that in the laboratory the haemoglobin content of the blood varies inversely with the oxygen content of the surrounding water, though the extent to which it does so may be influenced by other factors such as temperature, available iron, vitamin B_{12}, duck faeces and general level of nutrition. More recently, Chandler (1954) has shown that there exists in nature a general inverse correlation between the oxygen content of the surrounding water and the haemoglobin concentration in the blood of several species of *Daphnia*. It seems from this that it is possible to use the haemoglobin index of a population as a rough measure of the oxygen in the surrounding water. As the water in the waste tank was rich in nutritive material, constantly renewed from the filter beds, it is likely that most of the fluctuations in haemoglobin content were due to fluctuations in the oxygen content of the water and not to variations in the other factors which are known to affect haemoglobin synthesis.

During the period when the striking gain of haemoglobin was taking place the population was increasing rapidly so that the lowering of the oxygen content of the water which caused the gain of haemoglobin was almost certainly due to the increase of the population. Thus the haemoglobin content of the animals was to some extent proportional to the crowding that they were experiencing. Such a relation between crowding and haemoglobin content could only apply when a species was the dominant

Table 4. Daphnia magna *at Hampton, 1953*

	Population composition			Females with parthenogenetic eggs						
						Haemoglobin content				
Date	% females with eggs	% females ephippial	% male	Mean length (mm)	Mean egg number	female	male	*Colacium* index	Peritrich index	Rotifer index
3 Mar.	50	0	0	3·38	5·8	27	—	0	1	0
17 Apr.	90	0	0	3·66	51·2	15	—	21·5	0	0
21 Apr.	90	0	0	4·06	62·7	15	—	17·4	0·3	0
1 May	90	0	0	4·11	63·7	15	—	25·3	0·1	0
5 May	90	0	0	3·89	51·5	16	—	26·9	—	0·01
12 May	9	0	18	4·29	48·9	25	—	3·6	0	0
19 May	5	19	45	3·11	6·0	68	126	1·5	0·01	0
29 May	3	0·5	3	2·96	2·2	108	143	11·3	20·2	0
5 June	24	1	19	3·11	3·6	88	131	5·3	1·0	0
12 June	60	1	26	2·97	4·2	86	128	8·5	1·0	0·05
19 June	56	2·3	3·3	2·82	3·1	95	135	2·8	0·15	+
26 June	84	0·7	4·3	3·00	7·7	72	128	1·0	31·9	26·6
3 July	33	0	12	2·76	6·9	77	140	1·9	1·0	2·0
10 July	73	0·3	3·7	3·06	13·1	46	67	1·5	6·7	0·1

form in a locality. In a more natural population, in a pond for instance, there would be a much greater variety of animals, and fluctuations in their numbers would outweigh the fluctuations in the daphnian population. There is often rooted vegetation in a natural pond which would influence the oxygen content of the water by photosynthesis; there was no such vegetation in the settling tank.

Photosynthesis by planktonic algae is also important in determining the oxygen content of natural waters. Oxygen production by algae will be at its highest in summer when the light intensity and day length are at their greatest and the temperature is high. Chandler has shown that *D. obtusa* Kurz from several ponds is red in winter and pale in summer. She measured the oxygen content of the water in these ponds and showed that there was less oxygen in winter. Some of these ponds did not have rooted vegetation but contained abundant algae. The populations of *D. obtusa* in these ponds did not at any time reach the density of the population of *D. magna* in the settling tank (Chandler, personal communication).

It seems that haemoglobin formation cannot be regarded as a seasonal phenomenon, the main factor influencing it being the oxygen content of the water. One important factor influencing the oxygen content of the water must be the ratio between the density of the daphnian population and the density of planktonic algae. When populations are moderate or sparse and planktonic algae abundant the oxygen content of the water will be high and the haemoglobin content of *Daphnia* low. When populations are dense the planktonic algae will be reduced and the dissolved oxygen will become low; the haemoglobin content of *Daphnia* will then be high. The settling tank was rich in algae on 17 April 1953 when the water was coloured green, mainly by a species of *Chlamydomonas*; this persisted until 12 May but after this the water was much paler. Thus, apart from lowering the oxygen content of the water by its own respiration, *D. magna* was reducing the numbers of algae in the water. The low oxygen content in winter of the ponds examined by Chandler may be explained by the sparsity of algae at this time. However, the situation may not be as simple as this, for there are other factors which affect the oxygen content of water, such as temperature, and more especially the organic matter which may be in suspension or in the bottom layer. It would be possible to find ponds with abundant algae in which the oxygen content of the water was low; in such a situation a sparse population of *Daphnia* would be red with haemoglobin.

EPIBIONTS

The principal objective in studying the epibionts during 1953 was to see if the swarming of the motile stages of *Colacium vesiculosum* occurred again, and to see if a decrease in *Colacium* once more coincided with an increase of the rotifer *Brachionus rubens*. *Colacium* was not found swarming again, although the index did increase up to 5 May (Fig. 5). The drop in index which followed was probably due to the great increase in the numbers of the host. There was no increase in the rotifer population until 26 June and even then the number of rotifers per female *Daphnia magna* was much lower than in 1952. It seems probable that the decrease in *Colacium* recorded in 1952 was not entirely due to the increase in the rotifer population, even though both occurred simultaneously.

The two years were also different in the behaviour of the peritrich populations. In 1952 there was a general increase in numbers per host during the period of observation. In 1953 there were two short outbursts when peritrichs were abundant. In the first (29 May) the species responsible were *Intrastylum invaginatum* f. *daphniae* and *Rhabdostyla pyriformis*. In the second (26 June) a *Carchesium* species was present in large numbers; a few specimens of the earlier species were also found. This succession of species agrees with that found in 1952.

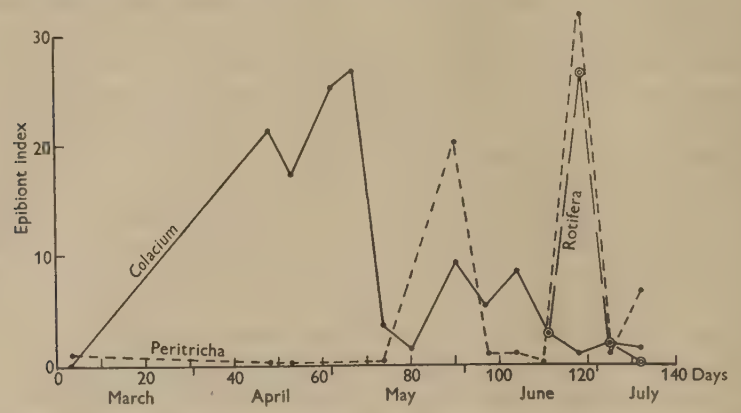

Fig. 5. Density of epibionts on *Daphnia magna* in spring and early summer 1953.

During the first peritrich outburst a sample of fifty females of *Daphnia magna* was examined to see if there was any relationship between the numbers of *Colacium* and the number of peritrichs on the carapace. Fig. 6 shows that the general rule is for an animal heavily coated with *Colacium* to carry fewer peritrichs than a lightly coated animal. It appears that when the epibiont population is dense there is competition for space on the carapace. In 1952 some laboratory observations were made on the effects of light on these epibiotic populations by placing *D. magna*, which had been reared in the laboratory free from epibionts, in dishes with a measured volume of water from the waste tank. The procedure was as follows. Six crystallizing dishes were each supplied with 90 ml of tapwater and 4 ml of the dark green water from the waste tank containing motile forms of *Colacium*, peritrich swarmers and rotifers. Ten first-instar young of *Daphnia magna* were added to each of four of the vessels, two of which were placed in front of a mercury vapour fluorescent lamp so as to be continuously illuminated, the other two being placed in a dark cupboard. No animals were added to the other two dishes; one was placed in the light and one in the dark. After four days the dishes were examined. In the cultures kept in continuous light the cladocerans were thickly and evenly coated with *Colacium* and no peritrichs were to be found; each animal carried six or eight rotifers. The cultures kept in the dark provided a striking contrast: *Colacium* was very sparse on the animals whilst peritrichs were abundant, particularly on the head; again each animal carried six or eight rotifers. In the vessels to which no cladocerans had been added, the one kept in the light had a thick coat of *Colacium* on the bottom, the water was quite clear. In the vessel kept

in the dark there was a sparse coat of *Colacium* on the bottom and many of its motile stages swimming about in the water. There were more peritrichs in the vessel kept in the dark. Thus by shifting the advantage in competition, in this case by light, the simplest available means, either *Colacium* or the peritrichs may become the dominant epibiont. *Brachionus* does not appear to be affected by the competition between *Colacium* and the peritrichs; probably its large size compared with the other two forms enables it to attach itself to *Daphnia* whether the smaller epibionts are present or not. *Colacium* was also found attached to the surface of the rotifer and more rarely to the

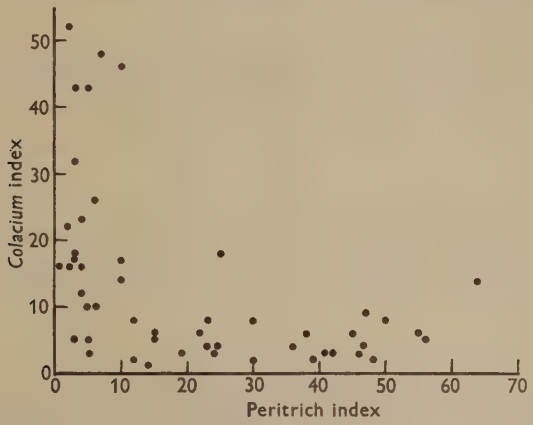

Fig. 6. Relation between the densities of *Colacium vesiculosum* and peritrichs on *Daphnia magna*.

stalks of *Carchesium*. We thus have *Colacium* in the motile form being eaten both by *Daphnia* and by *Brachionus*, and using both of these as substrata for attachment. The peritrichs were too small to ingest *Colacium*. The relations between the various epibionts found during the two years are summarized in Fig. 7.

OTHER SPECIES OF *DAPHNIA* IN THE TANK

The other species found in the tank were *Daphnia pulex* (De Geer), *D. obtusa* Kurz, *D. longispina* O. F. Müller and *D. curvirostris* Eylmann. They were not all found together and were never present in such great numbers as *D. magna*. On 21 April 1953 the first three were found together with *D. magna*. Conditions at the time were very favourable for parthenogenetic reproduction; one female of *D. magna* was carrying 108 eggs, the highest number ever recorded for the species (Bourguillant de Kerhervé (1927) records 105 in a cultured animal). The other species were also producing high egg numbers; the highest found were *D. longispina* 73, *D. obtusa* 57, and *D. pulex* 38. *Colacium vesiculosum* was found sparsely on all three of these species. On this same date copepods (*Cyclops* sp.) were abundant and were heavily coated with the peritrich *Epistylis anastatica* L., two specimens of which were found attached to *Daphnia pulex*. This is an unusual occurrence and may have been due to the high density of the peritrich on its more usual host.

In samples in which *Pansporella perplexa* was found infecting *Daphnia magna* the only other species present was *D. curvirostris*. More than 500 specimens were examined before one of this latter species was found with the amoeba in its gut, and even then only a single specimen of the parasite was found. It is clear that there is some specific difference which makes *D. curvirostris* less liable to infection than *D. magna*. The nature of this difference is unknown.

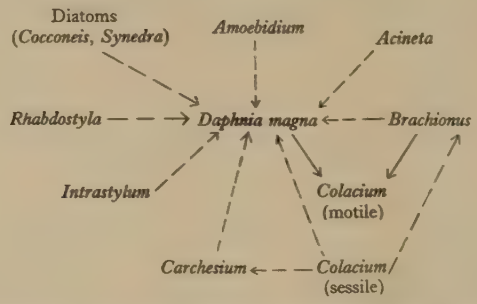

Fig. 7. Relations between epibionts on *Daphnia magna* at Hampton. Dotted lines go from epibiont to substratum, solid lines from predator to prey.

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SUMMARY

1. A description is given of the fluctuations in population composition, size of parthenogenetic females, egg production, haemoglobin content and density of epibionts on the carapace in a population of *Daphnia magna* in a sludge settling tank at Hampton Waterworks.

2. In the early summer the size of the parthenogenetic females and the egg production fluctuated together, while egg production and haemoglobin concentration fluctuated inversely. In winter both haemoglobin concentration and egg production were low.

3. Males produced more haemoglobin more quickly than females, they also lost it more quickly.

4. Other species of *Daphnia* found in the same settling tank were *D. curvirostris*, *D. obtusa*, *D. pulex* and *D. longispina*. On one occasion the last three were all taken together with *D. magna*.

5. The epibionts recorded were *Colacium vesiculosum*, *Rhabdostyla pyriformis*, *Intrastylum invaginatum* f. *daphniae*, *Carchesium* sp., *Acineta* sp., *Amoebidium parasiticum*, *Cocconeis placentula* and *Synedra* sp. *Epistylis anastatica*, normally epibiotic on copepods, was found sparsely on *Daphnia pulex*.

6. There was an inverse relation between the density of *Colacium* and that of peritrichs on the carapace of *Daphnia magna*.

7. Infection with an amoeboid parasite, *Pansporella perplexa*, was found. The degree of infection at different ages and reproductive states was examined. A specific difference was found in the degree of infection of *Daphnia magna* and *D. curvirostris*, the former being heavily infected and the latter practically uninfected.

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THE ECOLOGY OF THE BRITISH FRESHWATER LEECHES

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(With 4 Figures in the Text)

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INTRODUCTION

Many authors have made passing reference to the habits and habitats characteristic of the various British species of freshwater leeches, but none has attempted a systematic investigation of the ecology of the group. In other countries three papers have been published dealing wholly or mainly with the ecology of the local *Hirudinea*. These are by Pawlowski (1936), Bennike (1943) and Sandner (1951). Pawlowski (1936) collected from fifty-seven stations in the Polish Lake Wigryseen and in neighbouring smaller bodies of water. Ten of the thirteen species he collected are also found in Britain, so his results are of interest. He tackled the ecological problem in three ways. First, he recorded all possible information about the food habits of his leeches; secondly, he related the leech fauna to the type of substratum; and thirdly, he classified his habitats as eutrophic, dystrophic or oligotrophic, and considered which species of leech occurred in each type. Sandner, a pupil of Pawlowski, carried out a more extensive survey in the county of Lodz, in Poland, classifying his habitats in a rather arbitrary way into tarns, small ponds, fish-ponds, peat-pools, etc. He also made a number of physico-chemical observations on the water, and attempted to relate these to the presence or absence of certain species of leech. Bennike (1943) sampled 215 habitats scattered over the whole of Denmark, and attacked the problem mainly from the physical and chemical standpoints. He measured certain selected characters of the water in a proportion of the places visited, and related these to the species present. None of these workers used quantitative sampling methods, but Bennike was forced to conclude that 'it is not the qualitative but the quantitative composition of the fauna that characterizes the various types (of fresh water)'. It was therefore decided that an attempt would be made to study the ecology of leeches in Britain by making quantitative collections.

From a study of the above-mentioned papers it was thought that in all probability the most important single factor determining the distribution of leeches would prove to be the distribution of the appropriate food organisms, but clearly it was impossible

to study the problem from this angle, since each food animal would have required a separate investigation. It was therefore decided to try and establish a relation between the physico-chemical factors of the environment and the various species of leech, and then look for an explanation of this relationship in terms of food organisms. The chemical factors chosen for study were those regarded by Strøm (1928) as important in the classification of bodies of water. He recognized three main categories of lake—eutrophic, oligotrophic and dystrophic. The waters of the eutrophic lakes are characterized by an abundance of calcium, nitrogen and phosphorus, by the absence of brown colouring caused by humic acids, and by the presence of oxygen-consuming substances in solution. The oligotrophic waters have a low content of calcium and nutrient salts, no brown colouring matter, and a slight oxygen consumption. The dystrophic waters are similar to the oligotrophic, but are coloured brown by the presence of humic acids.

Sandner (1951) and Bennike (1943) both imposed a topographical classification upon the fundamental oligotrophic–dystrophic–eutrophic classification of earlier workers, e.g. eutrophic ponds were considered separately from eutrophic lakes. This seemed undesirable, since there is no sharp dividing line between a lake and a pond. Moreover, preliminary observations in Berkshire suggested that the size of a body of water was of secondary importance in determining its leech fauna, so it was decided to plan the survey so as to determine first and foremost the physico-chemical factors of the water, and to consider size only where this seemed to explain some important difference in leech fauna.

METHODS

(*a*) *Choice of methods*

In order to recognize the distinction between the three kinds of standing water, it was necessary to estimate the amount of base present. Ideally, separate estimations of calcium, magnesium, nitrogen, phosphorus and potassium would have been made, but this was considered impracticable. Two alternatives suggested themselves: (i) total hardness measured against a standard soap solution, or (ii) total alkalinity, by titration against standard acid.* Preliminary tests indicated that both methods gave a useful indication of the relative amounts of calcium and magnesium present in different habitats, but the total alkalinity titration was found to be quicker and more precise, and was therefore adopted. Strøm (1928) showed that only exceptionally are waters which are rich in calcium and magnesium also deficient in nitrogen, potassium and phosphorus, so it was thought that this titration would give a fair indication of the abundance of all these ions. A high figure would suggest a eutrophic condition, a low figure oligotrophic or dystrophic.

Following Strøm's (1928) assertion that dystrophic waters are coloured brown, the 'brownness' of each sample was measured by the technique of Ohle (1934), using a solution of methyl orange as the standard. Another factor separating the oligotrophic from the dystrophic condition is the proportion of organic matter in the bottom deposits. Following Bennike (1943) the evaluation of this factor was omitted in

* The method of Betz & Noll (1950) for estimation of calcium by titration against sodium versenate had not been developed when this survey was planned.

favour of the determination of the oxidizable (presumably organic) matter in solution in the water, using potassium permanganate, because the present writer is of the opinion that this figure is more characteristic of a body of water as a whole and has the additional merit of indicating organic pollution.

It was thought likely that peaty bottom deposits would have a lower pH than the bottom deposits of eutrophic waters, so a glass-electrode pH meter was used to determine the pH of the mud, while the pH of the overlying water was measured at the same time in order to find out the relation, if any, existing between the two.

It was thought unnecessary to measure the pH and the colour of running water, since these measurements were intended only as indications of the presence or absence of dystrophic conditions in standing water, and would not be expected to reveal anything important about the character of the river. The total alkalinity was measured at each station, and the dissolved organic matter was estimated when organic pollution was suspected.

There was little opportunity to exercise choice in the matter of habitats to be sampled. Two laboratories were used for the water analyses, the Zoology Department of the University of Reading, and the laboratories of the Freshwater Biological Association, near Windermere. As far as possible, all places likely to contain leeches within a radius of about ten miles of each of these centres were investigated both chemically and faunistically. In order to minimize errors caused by annual and diurnal changes in the environment and the fauna, collecting was limited to the months of July, August and September, and each station was visited between 11 a.m. and 3 p.m. Experiments were conducted to decide whether one water sample, or several, were required to give a picture of the conditions in a pond or small lake, and it was found that the variation from one part to another was usually slight, and that one sample would suffice. This view was justified when it was found that the figures obtained for total alkalinity in the tarns in the Lake District in July 1952 were in most cases close to the figures obtained by Macan in August 1948 (Macan 1950).

For quantitative methods of collecting leeches, the choice lay between methods based on units of area, and methods based on units of time. Area was rejected, because a unit area of one kind of substratum is in no way comparable with a unit area of another kind of substratum. For instance, a square metre of bullrushes may contain leeches among the roots, and among the leaves at all levels from the surface of the water to the bottom, but a square metre of stony bottom, devoid of vegetation, will provide shelter under the stones, and at no other level. The technique of collecting for a standard time has been successfully used by Macan (1950) in his study of the ecology of the Mollusca. Despite the objections cited by Sandner (1951) it may be fairly claimed that the method enables one to obtain at least an approximate idea of the relative abundance of leeches in the various habitats.

(*b*) *Details of methods*

The water and mud samples were taken from the littoral zone, over the substratum which seemed on inspection most nearly representative of the body of water as a whole. They were analysed immediately on return to the laboratory, and always on the day of collection.

Table 1. *Resul*

Stations are arranged in order of total alkalinity; a 1 h, and that the figures have been doubled for comparison. † indicates that juve s for this species in this locality. Heavy type indicates the species most numerous in

		$KMnO_4$ (mg/l.)	Colour	pH mud	*geometra*	Total (excluding *Haemopis* and *Hirudo*)	
1	Heath pond	46	12	6·4	—	0	
2	Queensmere	47	22	6·2	—	9	
3	Woodley S.	77	4	6·8	—	30	Oligotrophic
4	Milk cart	65	52	5·3	—	0	and
5	Welshman's	212	46	4·9	—	0	Dystrophic
6	Pullen's	121	34	6·7	—	30	
7	Pingewood	69	24	6·9	—	87	
8	Bearwood	56	24	6·5	—	75	
9	Farley	70	30	6·1	—	76	
10	Aldermaston N.	67	18	6·8	—	112	
11	Woodley N.	54	10	7·0	1	85	
12	Oakfield	57	30	7·4	—	293	
13	Colman's N.	60	8	7·0	—	59	
14	Crosfield	54	8	7·0	—	36	All Eutrophic
15	Colman's S.	100	34	7·0	—	40*	
16	Aldermaston S.	55	10	6·3	—	72*	
17	Whiteknights	55	20	7·3	—	73	
18	Cranemoor	88	10	7·4	—	198	
19	Maiden Erlegh	79	34	7·9	—	90	
20	Wokefield	88	12	7·3	—	174	
21	Waterworks	35	6	7·1	—	40	
22	Grazeley Green (Temporary)	98	40	6·6	—	92	
RUNNING WATER							
23	Foudry Brook	139	—	—	—	101	Fast
24	Blackwater	—	—	—	1	31	Slow
25	Colman's S.	100	—	—	—	104*	Fast
26	Cow Lane S.	182	—	—	—	34*	Very slow
27	Loddon	—	—	—	—	42*	Moderate
28	Pang	—	—	—	8	250	Moderate
29	Cow Lane N.	—	—	—	—	64	Very slow
	Total				10	2297	

nd standard collections of leeches for 1 h, in the Lake District

E. testacea	*Dina lineata*	*Haemopis sanguisuga*	*Hirudo medicinalis*	*Glossiphonia complanata*	*G. heterоclita*	*Batracobdella paludosa*	*Hemiclepsis marginata*	*Theromyzon tessulatum*	*Helobdella stagnalis*	*Piscicola geometra*	Total (excluding *Haemopis* and *Hirudo*)	
—	—	—	—	§	—	—	—	§	1	—	9†	
—	—	—	—	—	—	—	—	—	—	—	0	
—	—	24	—	39	21	—	—	—	72	—	299****	
—	—	39	—	25	—	2	—	—	§	7	64*****	
—	—	—	—	—	—	—	—	**2**	—	—	4	Oligotrophic
—	—	—	—	—	—	—	—	1	4	—	17	and
—	—	—	—	4	—	—	—	2	—	—	12	Dystrophic
—	—	—	—	—	—	—	—	—	—	—	†	
—	—	56	—	1	—	—	—	—	2	—	9	
—	—	—	—	3	—	—	—	—	4	—	13	
—	—	34	†	11	—	—	—	6	9	—	78**	
—	—	12	†	—	—	—	—	—	—	—	0	
—	—	—	—	—	—	—	—	—	—	—	0	
—	—	36	—	1	—	—	—	2	**13**	—	28**	
—	—	—	—	3	—	—	—	1	**6**	—	11†	
—	—	8	3	—	**21**	—	—	1†	4	—	26	Intermediate
—	—	4	—	—	—	—	—	—	**2**	—	2	between
—	—	4	—	—	—	—	—	—	**32**	—	32	Dystrophic
—	—	—	—	—	—	—	—	—	—	—	10†	and
—	—	—	—	2	2	—	—	3	**36**	—	49†	Eutrophic
—	—	—	—	6	—	—	—	2	**22**	—	34	
34	—	—	—	—	—	—	—	2	—	—	36	
—	—	—	4	—	—	—	**4**	1†	3	—	8†	
—	—	4	2	2	—	—	2	4	**6**	—	14	
—	—	—	—	**28**	—	—	—	1†	10	—	39†	
—	—	—	—	1	—	—	—	—	—	3	20	
—	—	—	—	5	—	—	—	—	1†	—	17†	All fast
—	—	—	—	—	—	—	—	—	2	—	36	flowing
—	—	—	—	4	—	—	—	—	2	—	110	
34	0	221	9	135	44	2	6	28	231	10	977	
22	16	287	9	524	109	8	56	71	1150	20	3274	
—	—	2	—	2	—	—	—	—	**6**	—	14	
—	—	24	—	16	6	—	—	—	16	—	60	
—	—	—	—	—	**15**	—	—	—	—	—	27	
—	—	—	—	—	—	—	—	—	**50**	—	58	
—	—	—	—	21	—	—	—	—	—	—	120	
—	—	—	—	2	—	—	—	—	—	—	7	
—	—	—	—	**11**	—	—	—	—	—	7	23	
—	—	—	—	**2**	—	—	—	—	—	—	4	
—	—	—	—	**10**	—	2	—	—	§	§	14	
—	—	16	—	—	—	—	—	—	—	—	16	
—	—	23	—	—	—	—	—	—	—	—	0	
—	—	36	—	—	—	—	—	2	—	—	11	
—	—	—	—	1	—	—	—	—	**13**†	—	17	

' collecting if more than one. Other symbols as in Table 1.

Total alkalinity was estimated by titrating a 50 ml sample of the water against 0·02 N sulphuric acid, using xylenecyanole-methyl orange as indicator. The result was expressed in the conventional manner, as mg $CaCO_3$/l. and calculated to the nearest mg. The colour of the water was measured by placing 50 ml of filtered sample in a Nessler tube, and 50 ml distilled water in a second Nessler tube. Methyl orange solution made up at a strength of 10 mg/l. was added to the distilled water until a colour match was obtained; every ml of methyl orange solution used represents 20 Ohle units. The potassium permanganate consumption was determined by taking 20 ml of filtered sample, making up to 100 ml with distilled water, and adding 5 ml 20% sulphuric acid, then boiling exactly 10 min with 10 ml 0·01 N-$KMnO_4$. The amount of permanganate remaining unused was ascertained by titrating against 0·01 N sodium oxalate, and from this was calculated the amount used during 10 min boiling. The result was expressed as mg $KMnO_4$/l., to the nearest mg. For further details of this method see Bennike (1943). The pH of the mud and of the water were determined with a Doran glass-electrode pH meter, used according to the maker's instructions.

The routine devised for making quantitative collections of leeches was as follows. On arriving at a body of water, a visual estimate was made of the number of major habitats in the littoral region, e.g. *Typha* reedbed, *Juncus* bed, stony shore, sandy shore. Collecting was then carried out for a standard time, which was divided between the habitats roughly in proportion to their areas. In the Reading district the standard time adopted was 2 h, but where a habitat was very small and uniform, collecting was stopped after 1 h and the numbers of leeches doubled for purposes of comparison. In the Lake District, however, the habitats tended to be more uniform, and the leeches less abundant, so that 1 h was adopted as the standard time, with $\frac{1}{2}$ h for the smaller bodies of water.

RESULTS AND DISCUSSION

(*a*) *General*

The geographical locations of the stations visited are shown on Figs. 1 and 2. Twenty-nine stations are situated in Berkshire, and twenty-nine in the Lake District.

Of all the physical and chemical determinations, that of the total alkalinity gave the most useful correlations between the nature of the water and the leech fauna. The stations on Tables 1 and 2 were arranged in order of total alkalinity, and without further analysis it is possible to discern the main trends of the distribution, *Erpobdella octoculata* being the most numerous leech in soft waters, and *Helobdella stagnalis* in hard waters. In Berkshire the range of total alkalinity is from 14 to 280, while in the Lake District the range is only 8 to 59. We may therefore regard the southern collecting ground as a predominantly hard-water area, and the northern as a soft-water area. The numbers of *Haemopis* and *Hirudo* collected are not included in the totals, as these species were not encountered in the normal routine of collecting, but had to be specially looked for. The numbers of other leeches taken in the south works out at 39·6/h, while the corresponding figure for the north is only 25·7/h. Clearly, then, leeches are more abundant in the southern, hard-water area.

There are at least two ways of analysing the results. One is to consider the various

types of habitat, and to try to deduce the typical fauna of each. The other is to list each species separately, and to consider what are the optimum environmental conditions. The two methods are complementary, and each will be attempted in the following sections.

Fig. 1. Sketch map of the Berkshire collecting area, showing running water, lakes, and ponds, the southern limit of the chalk, and the plateau gravel (stippled).

(*b*) *The various habitats, and their leech populations*

There is no sharp dividing line between the more productive and the less productive waters, either in Berkshire or in the Lake District, so that one can only draw an arbitrary dividing line, calling those below the line eutrophic, and those above the line dystrophic or oligotrophic. From a consideration of the geology of the district, and of the general flora and fauna, as well as the numbers of leeches, it would seem reasonable to draw such a line between stations 6 and 7. We may then define the eutrophic waters of Berkshire as those having a total alkalinity of 65 or over, a permanganate consumption not greater than 100, and colour never more than 34 Ohle. The highest figures were obtained only in polluted localities.

Of the sixteen stations which are thus defined as eutrophic, twelve have a similar fauna in which *Helobdella stagnalis* is the most abundant leech, and *Erpobdella octoculata*, *Glossiphonia complanata*, *G. heteroclita*, *Hemiclepsis marginata* and *Theromyzon tessulatum* are usually present (Table 3). There remain four stations in which the fauna is distinctly different, numbers 9, 15, 16 and 22. When the eutrophic stations are arranged in order of size, it is seen that these four stations where *Helobdella* is not the most numerous leech are also the four smallest, i.e. are ponds rather than small lakes.

Of the stations sampled in the Lake District, none fits the definition of eutrophic

as applied to the Berkshire stations, because none has an alkalinity of 65 or over. However, on the same basis of general considerations as before, it is convenient to draw a line between stations 40 and 41 in Table 2, separating those habitats with a total alkalinity of 18 or more from those with a total alkalinity of less than 18. Below the line, the most numerous leech in seven of the twelve stations where leeches occur is again *Helobdella*, with *Theromyzon* and *Glossiphonia complanata* also present

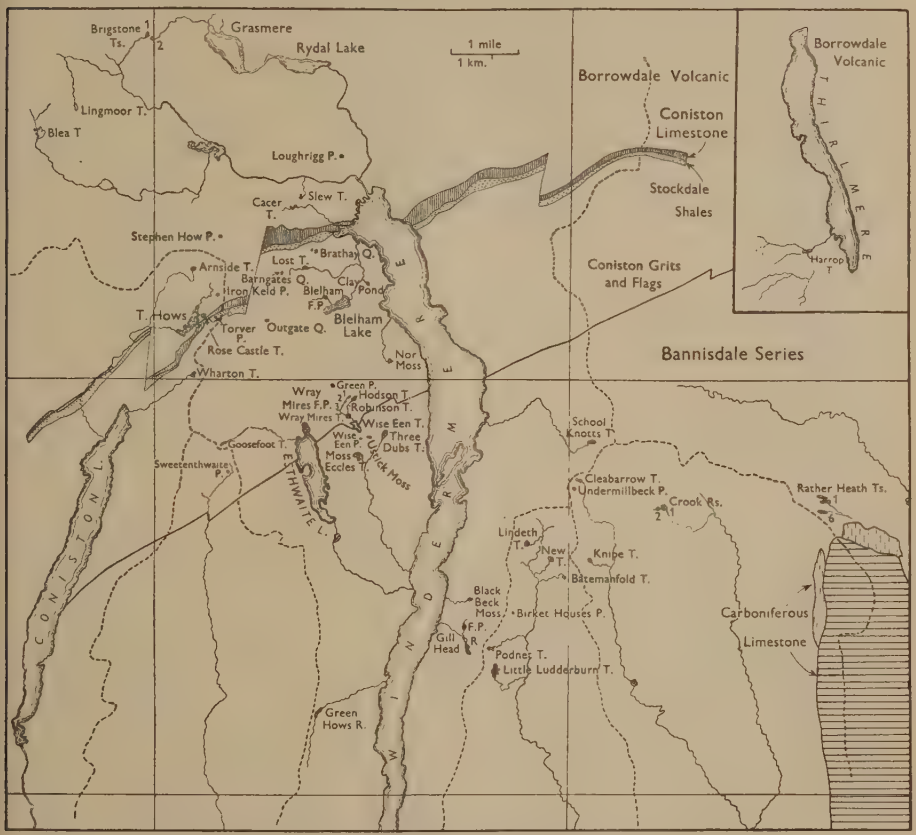

Fig. 2. Map of area studied in the Lake District, with solid geology and drainage areas. T = tarn, P = pool. (From Macan 1950.)

in six of them. The number of habitats differing from this pattern is rather large, and it is suggested that the stations in this group are variable in their character for the following reasons. Hard waters are usually eutrophic and soft waters either dystrophic or oligotrophic, but those of intermediate total alkalinity are not strongly predisposed to any of these categories. The result is that other factors, such as shape and size of the basin, and the nature of the surrounding vegetation tend to increase or decrease the productivity, and stations in this intermediate range of total alkalinity vary between moderately dystrophic and moderately eutrophic.

There is again a correlation between the size of the basin and the predominance of *Helobdella*, for if the stations in this group are divided into those of surface area over 10000 sq.yd and those not, then *Helobdella* is the most numerous leech in five out of six of those over 10000 sq.yd, and the most numerous leech in only two of the remaining eight (Table 4).

Table 3. *The leech fauna of eutrophic waters in Berkshire arranged in order of decreasing surface area*

Station	Area ($yd^2 \times 10^3$)	Most numerous	Second most numerous
8 Bearwood	212·0	*Helobdella stagnalis*	*Glossiphonia complanata*
18 Cranemoor	79·4	*H. stagnalis*	*Eropbdella octoculata*
11 Woodley N.	72·1	*H. stagnalis*	*E. testacea*
17 Whiteknights	60·1	*H. stagnalis*	*E. octoculata*
10 Aldermaston N.	55·2	*H. stagnalis*	*E. testacea*
12 Oakfield	37·8	*H. stagnalis*	*E. octoculata*
19 Maiden Erlegh	31·7	*H. stagnalis*	*E. octoculata*
20 Wokefield	9·4	*H. stagnalis*	*E. octoculata*
14 Crosfield	6·6	*H. stagnalis*	*G. complanata, Theromyzon tessulatum*
7 Pingewood	4·8	*H. stagnalis*	*G. complanata*
13 Colman's N.	4·4	*H. stagnalis*	*E. octoculata*
21 Waterworks	2·4	*H. stagnalis*	*G. heteroclita*
15 Colman's S.	2·4	*Erpobdella testacea*	*H. stagnalis*
9 Farley	1·9	*E. testacea, E. octoculata*	*G. complanata*
16 Aldermaston S.	1·3	*E. testacea*	*E. octoculata*
22 Grazeley Green (temporary)	0·9	*G. complanata*	*Dina lineata*

Turning now to stations 1–6, we find that the first three stations have a tendency to clearer water and less dissolved organic matter than the following three stations. On the basis of Strøm's work (1928) we might therefore be justified in calling the first three oligotrophic, and the others dystrophic. In the oligotrophic waters, *Erpobdella octoculata*, *Glossiphonia complanata*, *Hemiclepsis* and *Helobdella* are present at two stations, *Erpobdella testacea*, *Glossiphonia heteroclita* and *Theromyzon* at one station. To explain why leeches should be present in (2) and (3) but not in (1) it seems necessary to notice the size differences. It has been found in a number of instances that leeches seem to tolerate chemical conditions in a lake, which in a pond they cannot do. A similar correlation between small size of basin and absence of *Helobdella* has already been noted. Welshman's pond (5) is an extreme example of dystrophic conditions, with dark water, much dissolved organic matter, and acid mud. Milk Cart (4) shows the same condition in less extreme degree. Neither has any leeches, except for a single horse leech found out of the water at (4). Pullen's pond (6) is situated on the fringe of heath country. It is fed by a stream draining plateau gravel, but is itself on clay, and surrounded by dense oakwoods. It may be regarded as dystrophic, but the organic matter which accumulates is derived largely from oak trees, rather than from heather and birch. *Erpobdella octoculata* is the most numerous leech.

The stations from 30 to 40 (Table 2) all have *E. octoculata* as the most numerous leech, except that Moss Eccles (31) has no leeches at all. None of the stations has extremely dystrophic conditions comparable with those in Welshman's (5). Such

conditions would have been found in the peat pools of the Lake District but Dr Macan assured me that leeches were totally absent from this type of habitat, and for that reason they were not visited. On the basis of Strøm's work, previously quoted, we may arrange stations 30–40 in descending order of colour density (and descending order of dissolved organic matter where several stations have the same colour density) and interpret this as meaning that those near the top of the list are dystrophic and those near the bottom of the list are oligotrophic. This has been done in Table 5. The first five stations are fairly uniform in character, but the remainder are not, some being so productive as to be nearly eutrophic. One of the factors contributing to this difference is size, for Loughrigg (32) and Staveley (40) which are large, yielded good numbers of leeches and are obviously productive bodies of water, but do not differ very greatly in chemical composition from much smaller bodies of water such as Hodson (36) which is very much less productive. Table 5 brings out the fact that the dystrophic waters yielded fewer leeches and fewer species than did those in the oligotrophic group.

Table 4. *The leech fauna of 'intermediate' stations in the Lake District, arranged in order of decreasing surface area*

The space separates stations with a surface area of more than 10000 sq.yd from those which are smaller.

Station	Area ($yd^2 \times 10^3$)	Most numerous	Second most numerous
43 Esthwaite L.	100+	*Helobdella stagnalis*	*Erpobdella octoculata*
44 Blelham	100+	*H. stagnalis*	*Glossiphonia complanata*
46 Knipe	25·5	*H. stagnalis*	—
49 Rather Heath 1	25·2	*H. stagnalis*	*E. octoculata*
47 Podnet	22·3	*H. stagnalis*	—
48 Wharton	15·3	*E. octoculata*	—
45 New	10·0	*Glossiphonia heteroclita*	*H. stagnalis*
42 Arnside	10·0	—	—
53 Rather Heath 6	7·7	*H. stagnalis*	*Theromyzon tessulatum*
51 Cleabarrow	6·6	*E. testacea*	*T. tessulatum*
54 Crook Mill	6·3	*G. complanata*	*H. stagnalis*
50 Rose Castle	5·8	*H. stagnalis*	*G. complanata*
41 School Knotts	4·9	—	—
52 Crook Reservoir Upper	2·3	*Hemiclepsis marginata*	*H. stagnalis*

In summarizing the findings for standing waters, we see that eutrophic waters are seen at their best in Berkshire, and that with few exceptions they have a fauna in which *Helobdella* is the most numerous leech, accompanied by *Erpobdella octoculata*, one or both species of *Glossiphonia*, *Hemiclepsis* and *Theromyzon*. A similar fauna is found in a number of the harder waters of the Lake District. The oligotrophic and dystrophic moorland waters of the Lake District also have a characteristic fauna in which *Erpobdella octoculata* is the most numerous leech, and the next most abundant is either *Glossiphonia complanata*, *Theromyzon*, or *Helobdella*. Large numbers of *Haemopis* may often be taken in the vicinity of these waters. Very dystrophic conditions which occur in peat pools, either on the fells of the Lake District or on the plateau gravels of Berkshire, exclude leeches (Table 6).

Changes in both the environment and the fauna occur around total alkalinities of 18 and 60, and these have been taken as the dividing lines between (i) the soft,

oligotrophic and dystrophic waters, (ii) the intermediate group of stations where factors other than alkalinity swing the balance towards either dystrophic or eutrophic conditions, and (iii) the markedly eutrophic stations. Ohle (1934) suggested that for practical purposes the dividing line between soft, intermediate and hard waters should be at a calcium content of 9 and 25 mg/l. respectively, and Bennike (1943) placed the upper limit of dystrophic conditions at 9 mg CaO/l. When these figures are multiplied up to make them comparable with figures for calcium carbonate equivalent, they become 22 and 63 (Ohle), and 16 (Bennike), which are very similar to those arrived at in this survey.

Table 5. *Stations 30–40 arranged in descending order of colour density*

Station	Number of leeches	Average	Number of species	Average
	DYSTROPHIC			
37 Scale	Cocoons only		1	
31 Moss Eccles	0		0	
35 Wise Een	17	8	3	2·2
39 Wraymires	13		3	
38 Tarn Hows	9		4	
	OLIGOTROPHIC			
40 Staveley	78/2 = 39		5	
30 Three Dubs	9		4	
34 Gill Head	4		2	
36 Hodson	12	23·3	3	4·2
32 Loughrigg	300/5 = 60		5	
33 Windermere	64/4 = 16		6	

Next to alkalinity, area of the basin appears to be the most important factor in leech ecology. If two habitats have approximately the same type of water, but one is much smaller than the other, then if both have hard water, the smaller will be less likely to have *Helobdella* predominating, and if both have soft water, then the smaller will be less likely to have any leeches at all. A possible explanation of this phenomenon is that small bodies of water tend to be shallow, and may never stratify, so that an oxygen deficit in the hypolimnion, which is so important in the liberation of nutrient salts from bottom deposits may never occur. Thus *Helobdella*, which finds abundant suitable food and therefore flourishes, in hard-water lakes and tarns, is less likely to do so in hard-water ponds. In soft waters, where plant remains tend to accumulate as acid peat, the small body of water, by reason of its shallowness, is likely to have a greater amount of rooted vegetation per square yard of surface area than is a large body of water. Hence the acid, dystrophic conditions are likely to be intensified, and *Erpobdella octoculata* which often thrives in soft-water lakes, may be excluded from the pools.

The techniques for estimating colour and dissolved organic matter have proved effective in separating brown waters with a high content of organic matter from clear waters with a lower dissolved organic matter content, and it has been shown that the latter contain a greater number and variety of leeches, but to follow Strøm (1928) and call the clear, soft waters oligotrophic is not entirely satisfactory. Into this category come such lakes as Windermere, which is far from unproductive or oligo-

trophic. It is here that the limitations of the chemical approach become evident. Dr T. T. Macan of the Freshwater Biological Association has written (privately) that lakes such as Windermere are about a thousand times as productive as lakes such as Ennerdale, but the chemical differences are quite slight. More work is required before an adequate classification of these soft waters can be arrived at. In the meantime the term oligotrophic has been retained for want of a better.

Table 6. *A broad classification of the habitats with the leeches most characteristic of each*

	Characteristic leech	Station numbers
Very dystrophic	None	1, 4, 5, 31
Oligotrophic and dystrophic	*Erpobdella octoculata*	30, 32–40
Intermediate	*Helobdella* and others	41–54
Eutrophic	*Helobdella*	7–22
Sluggish streams	*Helobdella*	24, 26, 27
Fast streams, soft water	*E. octoculata*	23, 25, 55–8
Chalk streams	*Glossiphonia complanata*	28

The measurement of pH of mud proved less useful than other measurements as a guide to the nature of the habitat, but considered independently of the other factors, there is an undoubted relationship between the pH of the mud and the number of leeches present. The more alkaline the mud, the more leeches are obtained. This is shown in Table 7. The measurement of pH of water has proved of little value in this work.

Table 7. *The relationship between total number of leeches and the* pH *of the mud*

pH range	< 6·5	6·5–7·0	> 7·0
Average number of leeches per hour's collecting	18·7	28·3	73

While few of the results of this survey have been anticipated by Pawlowski (1936) or Bennike (1943), it is possible, by inspection of their data, to see that their figures are in agreement with the conclusions mentioned above. They both found that leeches were absent from extremely dystrophic localities, but that where conditions were only moderately dystrophic *E. octoculata* was usually to be found. Pawlowski found that in oligotrophic localities occurred the greatest number of species. Neither Bennike nor I have any evidence to support this finding, but it is possible that no truly oligotrophic localities have been investigated either in Denmark or in England. Bennike's tables show that *Helobdella* is present in every lake with a total alkalinity of more than 62 mg $CaCO_3$/l., but neither he nor Pawlowski realized that the distribution of this leech and that of *Erpobdella octoculata* are quantitatively complementary, with *Erpobdella* the most numerous leech in dystrophic localities and *Helobdella* the most numerous leech in eutrophic localities. The fauna of ponds was considered by Bennike independently of the fauna of lakes, and he found that the three species *Batracobdella paludosa*, *Haemopis sanguisuga* and *Dina lineata* occurred in ponds but not in lakes. The first two species named have been found in Windermere, so there is no British evidence to support Bennike's findings.

The leech fauna of running waters sampled in the Lake District is remarkably uniform. In each place *Erpobdella octoculata* is the most numerous; *Glossiphonia complanata* and *Helobdella* were each present in three out of four stations, and *Piscicola geometra* at one. In Berkshire there are three stations which have the same kind of leech fauna. Foudry Brook (23) and Colman's S. (25) are directly comparable with the Lake District streams because the speed of the water is such that the bottom consists of fairly large stones, under which *Erpobdella octoculata* shelters, often in large numbers. Organic pollution resulting in a permanganate consumption of up to 139 mg l. seems to favour this species, for it was most numerous in the Lake District stream with the highest content of dissolved organic matter, Black Beck (58), which is said to receive the sewage effluent from Hawkshead.

The Blackwater (24) and the Loddon (27) are broad sluggish rivers in which the collections were made in marginal vegetation. *Helobdella* is numerous, and the fauna generally resembles that of eutrophic lakes and ponds. The River Pang (28) drains the chalk, and abounds in the gastropod *Hydrobia jenkinsi* Smith. This probably accounts for the great numbers of *Glossiphonia complanata* present, and if it were not for this factor, the fauna would resemble that of the Lake District rivers. Cow Lane S. (26) must be described as foully polluted. Its fauna is that of eutrophic waters, with the addition of a good number of *Haemopis* which were observed to feed on the tubificids in the highly organic mud on the bottom.

Table 8. *Distribution in relation to total alkalinity in standing water; figures give the percentage of stations at which each species is found*

	Range of total alkalinity (mg l.)		
	8–17	18–60	61–242
Erpobdella octoculata	82	42	88
Glossiphonia complanata	50	42	62
G. heteroclita	8	10	62
Theromyzon tessulatum	33	47	75
Helobdella stagnalis	50	60	75

The picture which emerges of the fauna of running water is of slow waters having a fauna similar to that of eutrophic ponds and lakes, and of fast waters having a fauna in which *Erpobdella octoculata* greatly predominates, except where the water is exceptionally hard, when molluscs will be abundant and *Glossiphonia complanata* will thrive. Bennike's (1943) results agree well with these conclusions.

(*c*) *The various leeches and their habitat preferences*

(i) *Erpobdella octoculata* (L.)

As shown in the previous section, this species is most numerous in the softer waters of the Lake District, where the conditions range from dystrophic to almost eutrophic. It is not, however, by any means confined to this type of water, as it is present in fourteen of sixteen eutrophic habitats in Berkshire, although never the most numerous species. Its apparent absence from a number of the relatively hard waters of the Lake District is difficult to explain. The relationship between the occurrence of this leech and the total alkalinity of the water is summarized in Table 8. These figures refer to

standing water only. In running water which is sufficiently fast to scour the bottom, leaving a stony bed, *E. octoculata* is particularly abundant, and is the most numerous leech in all streams of this type. No station in running water was ever sampled without *E. octoculata* being taken. It will be seen from Table 2 that in certain larger bodies of water separate collections were made on the different types of substratum. The results indicate that *E. octoculata* is found much more often on stones than on vegetation, at least during the summer months (Table 9). The suggested explanation is that

Table 9. Erpobdella octoculata *as percentage of total catch, in different habitats*

	Habitat	Percentage of *E. octoculata*
Loughrigg tarn	Shaded stones	43
	Stones with *Littorella*	53
	Stones near reeds	44
	Reed bed	14
Esthwaite water	Stony shore	82
	Reed bed	18
	Dredged weed, 3–5 m	0
Streams	Black Beck (stony)	95
	Foudry Brook (stony)	90
	Blackwater (weedy)	10

the food organisms of this species, mainly chironomid and trichopteran larvae, are more abundant on stones than on vegetation. Both Pawlowski (1936) and Bennike (1943) made experiments in aquaria on the food preferences of the various species of leech, and these shed a good deal of light on the results of this survey regarding the distribution of the leeches. *E. octoculata* feeds mainly on chironomid, simuliid and trichopteran larvae, but Meuche (1937) mentions in addition ostracods, copepods and Cladocera. This type of food is found in even the softest waters, and helps to explain the predominance of *E. octoculata* in soft waters. Its macrophagous habits enable it to subsist on a predominantly arthropod diet, while those species which insert a proboscis and suck the body fluids are dependent on a supply of soft-bodied food organisms.

(ii) *Erpobdella testacea* (Savigny)

The range of distribution of this species is much more restricted than is that of *E. octoculata*. The latter occurred in forty-two out of fifty-nine stations sampled, while *E. testacea* was taken at only ten stations. The character which these ten stations have in common is that they receive their water mainly from plateau gravel. None of the stations draining mainly London Clay or valley gravel yielded this species.

According to the literature, *E. testacea* has exactly the same feeding habits as the other species of the genus. Its breeding habits are also similar, and it is difficult to find any reason for the very different distributions. Bennike (1943) found it in dystrophic localities which appeared to exclude *E. octoculata*, but otherwise found it to be less common than *octoculata* in all types of habitat. Sandner (1951) collected only 158 specimens of *E. testacea* compared with 1784 *E. octoculata*, and found it in only 24% of stations, while *E. octoculata* occurred in 88%. The corresponding figures

for this survey are 17% and 71%, so that the relative abundance of the two species is about the same in Britain and in Poland.

If food and breeding habits are similar in the two species, there must be some physiological difference to account for the restricted distribution of *E. testacea*. In a previous paper (Mann 1952) it has been suggested that *E. octoculata* normally prevents *E. testacea* from establishing itself, but if conditions are unfavourable to *octoculata*, then *testacea*, which is perhaps physiologically more resistant, becomes the dominant species. It is further suggested that conditions unfavourable to *octoculata* might be organic pollution in closed habitats, or mineral deficiencies in water drained mainly from plateau gravel.

Two other factors in the ecology of this species have been noticed. One is that habitats containing large beds of *Sparganium ramosum* can usually be relied on to yield good numbers of *Erpobdella testacea*, and the other is that habitats which would seem to be suitable for this leech, except that they tend to dry out in summer, contain instead the closely related *Dina lineata*. More information is required before the optimum habitat for this species can be defined.

(iii) *Dina lineata* (O. F. Müller)

The only habitat in which this leech was found during the survey was a pond at Grazeley Green (22). At a later date a specimen was found at Colman's Moor (13). The formal sampling was carried out in the summer of 1951, and there was plenty of water present, but in September 1952 only one-tenth of the bottom of the pond was covered by water. Consideration of rainfall figures suggests that in a really dry season the pond would dry out completely. Pawlowski (1936) took this species only from temporary ponds, and according to Kulajew (1929) it can survive seven months without free water, but Bennike (1943) found it mainly in running water, and others have found it in springs and lakes. The results of this survey support Pawlowski's view that temporary ponds are the characteristic habitat.

(iv) *Haemopis sanguisuga* (L.)

General information about the ecology of this species has been given by Mann (1954). In Berkshire, the only place where the leech was taken in considerable numbers was a foully polluted ditch referred to as Cow Lane S. (26). Here the leeches were found burrowing in the soil of the bank and sheltering in the leaf bases of *Sparganium*. In the Lake District the species was encountered much more frequently, invariably being found under stones, just above the water's edge. Here, during the summer months, it feeds on earthworms and deposits cocoons. During winter the leech congregates under large stones in 0·5–1 m of water. Because the leech was almost invariably found out of water, it was not encountered in the normal collecting routine. It was made the object of a separate timed collection, and the results expressed against a standard time of 1 h. It is not certain whether the dearth of specimens in Berkshire is real, or whether in the absence of suitable stones near the water's edge, it hides in the soil and vegetation and is more difficult to find. It does not seem to be restricted to any particular kind of water in the Lake District, but it is significant that

at stations 4 and 41 *Haemopis* was found near waters which contained none of the other species.

It is a macrophagous carnivore, devouring almost any animal tissue which can be drawn into its capacious crop. In the summer months much of its food is of terrestrial origin, so that it is able to thrive even in waters where suitable food organisms are scarce. Bennike found it most frequently in lakes, fairly frequently in ponds, and only occasionally in running water. Of the ten stations where it was taken in the Lake District, only two were of an area less than 10000 sq.yd. Sandner (1951) found it most frequently in tarns and peat pools, which supports my finding that it is more common in soft water than in hard.

(v) *Hirudo medicinalis* L.

This leech, which was once thought to be extinct in this country, has been rediscovered in a few localities such as the New Forest, and part of Wales. The staff of the Freshwater Biological Association knew of its occurrence in Staveley Reservoir (40) and School Knotts Tarn (41), but during this survey three new localities in the Lake District were added to this list. Since *Hirudo* swims rapidly towards any centre of disturbance in the water, the numbers taken in each locality have simply been recorded without any correction for the time factor, and not included in the totals. No correlations with the chemical features of the water have been attempted, but it may be noted that none of the stations where it has been recorded has an area of more than 10000 sq.yd.

This species is normally regarded as a mammalian parasite, but Blair (1927) recorded that the young leeches feed on frogs, tadpoles, and small fish, and Bennike (1943) confirmed this. Blair also remarked that the adult leeches suck the blood of cattle and horses which enter the water to drink, while Scriban & Autrum (1932–34) stated that *Hirudo* cannot reach sexual maturity until it has sucked the blood of a mammal. In Britain the leech is now known from the New Forest (Blair 1927), South Wales (Quick 1938), Norfolk (Professor H. Munro Fox private communication), Islay, Scotland (Reynoldson 1952), and the Lake District. Four of these localities are known to be uncultivated country where horses or cattle roam freely and might reasonably be expected to visit the ponds to drink, thus providing the opportunity for the leeches to obtain mammalian blood. It is possible that the decline in numbers of medicinal leeches in our ponds which has taken place in the last 200 years is associated with the closer control of horses and cattle, and the habit of watering them at troughs rather than at natural ponds. It is probable that the leech still survives in a fair number of localities where the older methods of cattle management persist.

(vi) *Glossiphonia complanata* L.

This species is found over the whole range of habitats, from the softest to the hardest waters. The relationship between its distribution and the total alkalinity is summarized in Table 8. Comparing this with *Erpobdella octoculata*, we find that *G. complanata* occurs less frequently than *E. octoculata* but shows the same drop in frequency in the middle range of alkalinity. This supports the idea that in these 'intermediate' tarns there is some factor not evaluated which is not conducive to leeches.

In running water the frequency of occurrence is higher, 82% of all stations. The stations where *Glossiphonia complanata* is the most numerous leech are Grazeley Green (22) which has the highest total alkalinity for standing water in Berkshire, the River Pang (28) which is the hardest stream sampled, and Crook Mill Pond (54) which is the hardest water sampled in the Lake District. In each case it was noticed that molluscs were particularly numerous. It may therefore be presumed that optimum conditions for this leech are presented by hard running water, and that hard standing water is the next most favourable. Table 10 shows that in Loughrigg the leech preferred stones to vegetation, and this suggests that the leech feeds on those species of mollusc found chiefly on stones. Since stony substrata are naturally more abundant in running water, it is not surprising that *G. complanata* is found more often in running water than in standing water.

Table 10. Glossiphonia complanata *as a percentage of total catch, in various habitats in Loughrigg Tarn*

	Percentage of population *G. complanata*
Shaded stones, north bank	14
Stones with *Littorella*, S.E.	20
Stones near reeds, N.E. corner	0
Reed bed, N.N.W. corner	0
Outflow stream, stony	17

All authors are agreed that gastropod molluscs form the chief article of food, the proboscis being inserted into the soft tissues and the body fluids extracted. Autrum (1936) recorded insect larvae and worms as part of the diet, but this is probably exceptional. Since molluscs are on the whole more plentiful in hard waters than soft (Boycott 1936), it is not surprising that the habitats where *G. complanata* is the most numerous leech are those with the hardest waters. Boycott also stated that conditions which favour freshwater molluscs in general are to be found in gently flowing, shallow streams which have a moderate but not excessive growth of plants, and this again fits in with the observation that *G. complanata* is found more often in running water than elsewhere, and is most abundant in the Pang, a river which exactly fits Boycott's description. These findings are supported by Pawlowski (1936) and Bennike (1943).

(vii) *Glossiphonia heteroclita* (L.)

The distribution of this species is more restricted than that of the other species within the genus. Whereas *G. complanata* is found in both hard and soft waters, and in running as well as standing waters, *G. heteroclita* is much more common in hard waters than in soft, and is never found in water with an appreciable current. In only one station, New Tarn (45), was it the most numerous leech present. This tarn yielded the greatest number of molluscs in the ecological survey of that group carried out by Macan (1950). The leech feeds on gastropods, being associated particularly with *Bithynia*. It occurs most frequently in the eutrophic lakes and ponds of Berkshire, and these are typically rich in molluscs. Bennike (1943) found occasional

specimens in rivers or streams, but noted that they were always among dense marginal vegetation where there was virtually no current. The absence of this species from running water may be related to its breeding habits. *G. complanata* lays its eggs in about three gelatinous cocoons which it attaches to the substratum, and then covers with its body. *G. heteroclita*, on the other hand, attaches its cocoons to the ventral surface of its body, and it is possible that this method is unsatisfactory in running water. *Erpobdella octoculata*, which is often very abundant in fast-running stony streams, lays its eggs in hard, flat cocoons which are firmly cemented to the substratum.

(viii) *Batracobdella paludosa* (Carena)

This is the second leech newly discovered in Britain during the course of this survey. It was first found in Aldermaston S. (16), a small, polluted, and very anaerobic pond which was in dense woodland, and received water from a stream which drained plateau gravel. Two specimens were later discovered in Windermere. Bennike (1943) found it in three localities, two of which were woodland ponds. Sandner (1951) collected it from nine localities, five of which were peat pools (Torfianki). In this country it has been found in numbers only in the small woodland pond, and it seems likely that its optimum habitat is a small body of water with an accumulation of humus. Blanchard (1894) recorded it as feeding on the gills of tadpoles. Bennike failed to confirm this. Others mention snails as the food organisms, but more evidence is required.

(ix) *Hemiclepsis marginata* (O. F. Müller).

The most striking aspect of the distribution of this leech is its scarcity in the Lake District. Only six specimens were found, at two stations which have almost the hardest water in the district. In Berkshire, however, the species occurs over a wide range of alkalinities, and is present in 62% of the eutrophic lakes and ponds. In running water it was found only in the two sluggish streams, Cow Lane S. (26) (foully polluted) and Colman's S. (25). *H. marginata* is a fish parasite which almost certainly attacks amphibians as well. Another fish parasite is *Piscicola geometra* but this is never found in small, overgrown waters, and only occasionally in open ponds. In these localities *Hemiclepsis* may be considered as replacing *Piscicola*. The scarcity of *Hemiclepsis* in soft waters is confirmed by Bennike's figures, as he found it in only 15% of those lakes with a total alkalinity under 78 mg $CaCO_3$ l., and in 62% of those lakes over that figure. Sandner found it in eight lakes, eight ponds, but only one peat pool. It seems reasonable to suppose that for *Hemiclepsis* the ideal habitat is a eutrophic one, presumably because it is here that the fishes on which it feeds, such as tench, roach, carp, and stickleback are found in greatest numbers.

(x) *Theromyzon tessulatum* (O. F. Müller)

This species seems to have become more abundant in Europe in the last ten to twenty years. Lukin (1929) reported it as rare in Poland, but Sandner (1951) found it in 12% of all localities examined. Harding (1910) stated that it was rare in the British Isles, but it turned up in nearly half of the stations sampled during this survey.

It is just possible that earlier collectors overlooked it, but it is difficult to see why this should be so when they had found most of the other species in good numbers. It occurs in both soft and hard waters, but more frequently in hard, as is shown in Table 8. The relative scarcity of leeches in the intermediate range of alkalinities, noted for other species, is not found here.

Theromyzon is a parasite of water fowl, a large number of web-footed and wading birds being mentioned as hosts. This being so, it is not surprising that it should be found in almost every type of aquatic habitat, for it is independent of the other aquatic organisms for its food. Only in running waters was it comparatively scarce. In this survey it has not been found in fast streams with a stony bottom but the river Pang yielded nine specimens, and this is a moderately fast river, with patches of vegetation mixed up with shoals of sand and large stones. Young individuals have been found mostly on vegetation, but the breeding adults were confined to the undersides of stones.

Table 11. Helobdella stagnalis *as a percentage of total catch, in various types of habitat*

Locality	Habitat	Percentage *Helobdella*
Loughrigg tarn	Shaded stones	45
	Stones with *Littorella*	20
	Stones near reed bed	0
	Reed bed	80
Esthwaite Water	East shore, stony	0
	Reed bed, S.E. shore	76

(xi) *Helobdella stagnalis* (L.)

The distribution of this leech is complementary to that of *Erpobdella octoculata*. Both are found in a wide range of alkalinities, but whereas *E. octoculata* is the most numerous leech of dystrophic waters, *Helobdella stagnalis* is numerically dominant in eutrophic waters. The relative abundance of these two species may therefore be used as an indicator of dystrophic and eutrophic conditions respectively. The relation existing between the occurrence of this leech and the total alkalinity is summarized in Table 8. In running water it is present in 73 % of the localities, but is the most numerous leech only in slowly moving waters. A consideration of the results of several separate collections in the different types of habitat within Loughrigg and Esthwaite Water shows that *H. stagnalis* is found more abundantly on vegetation than on stones (Table 11).

H. stagnalis is a sucking leech, provided with an unarmed proboscis for taking up fluids and fine particles. Bennike (1943) has suggested that it has external digestion, and records that it sucks chironomid larvae, *Asellus* and snails. Pawlowski (1936) also mentions a variety of insect larvae, as well as oligochaetes, and states that these are taken in preference to snails. Bennike compared the faunas of the various species of aquatic plants, and made a number of inferences regarding the preferences of the various species for various plants, but there seems to be a serious fallacy in his argument since he compared the fauna of *Potamogeton* in one lake with the fauna of

Glyceria in another, and there is no evidence to show why the differences should not be attributable to differences in the water. The same criticism applies to his analysis of habitats without vegetation. His figures show, however, that in four out of five habitats without vegetation *Erpobdella octoculata* was more numerous than *Helobdella*, but in five out of nine habitats with vegetation *Helobdella* was the more numerous. This lends some support to the conclusion reached previously, that in the same body of water *Erpobdella octoculata* prefers a stony substratum and *Helobdella* prefers vegetation, at least during the summer months. It has not yet been possible to relate these facts to the different distributions of the two species.

(xii) *Piscicola geometra* (L.)

Piscicola is a comparatively rare leech, being found at only five stations. It is confined to running water and to the wave-washed shores of fairly large bodies of standing water. In Windermere (33) seven specimens were found near the mouth of an inflowing stream, the Trout Beck. In North Lake, Woodley (11) one specimen was taken on the north-east shore, which was fully exposed to the prevailing wind. All other specimens were taken from running water, the greatest number being found in the River Pang (28). It seems, therefore, that this species is confined to habitats where the water is in constant motion.

P. geometra is the second fish parasite encountered, and attacks, among others, perch, bream and sticklebacks. In this country it has been found only on stones, but Bennike (1943) regarded it as belonging to the submerged vegetation of lakes. Sandner (1951) found it in large aggregations in certain fish ponds and 'natural waters', but all these writers are agreed that it differs radically from *Hemiclepsis* in not being found in small ponds. My own results suggest that the primary requirement is moving water with consequent good aeration, but Bennike has suggested that it cannot stand the high temperatures found in small bodies of water in summer. In support of this he quotes Herter (1932) who showed that *Piscicola* exhibits an abnormal type of behaviour, and finally ceases to move, at a temperature several degrees lower than for any other freshwater species investigated. Temperature and oxygen concentration are so closely related, that more critical laboratory experiments are required to determine which is the more important factor.

CONCLUSIONS

Fig. 3 illustrates the frequency of occurrence of eight species of leech in the various habitats dealt with. From it we see that four species of leech are found in every type of habitat, *Erpobdella octoculata*, *Glossiphonia complanata*, *Helobdella stagnalis* and *Theromyzon tessulatum*. Bennike (1943) reached the same conclusion regarding the first three species, but found *Theromyzon* restricted mainly to standing water. The remaining four species in Fig. 3 are restricted in their range of habitat: *Erpobdella testacea* was not found in soft water, *Glossiphonia complanata* was not found in running water; *Hemiclepsis marginata* was absent from soft waters and from fast running water, whereas *Piscicola geometra* showed a preference for running water. The leeches whose distributions are not shown are those which proved to be too rare for any conclusions

to be formed, or those that leave the water for part of the year, so that collections are unreliable.

It will be noticed that all leeches except *Piscicola* occur more frequently in hard waters than in soft or intermediate. It might be argued that this is a misconception resulting from the fact that hard waters were sampled for two hours, and the others for only one, but the fact that leeches are more abundant in hard waters than in soft has already been noted, and the author is firmly of the opinion that a further hour's collecting in the soft waters would not have resulted in the discovery of new species.

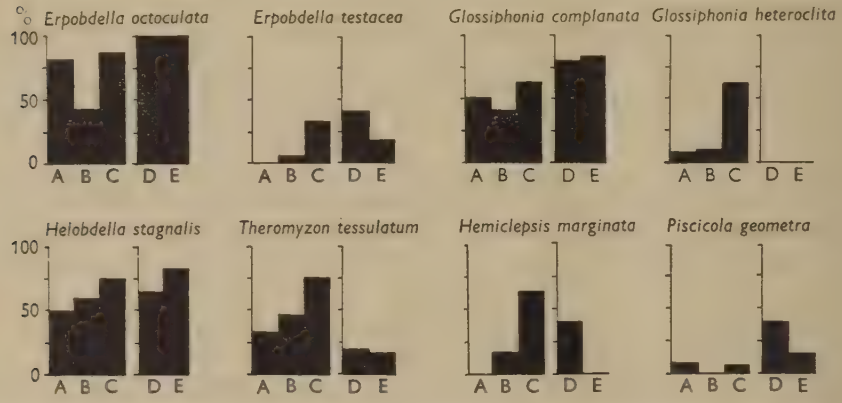

Fig. 3. The frequency of occurrence of various leeches in the different types of habitat. A, soft standing water, alkalinity 8–17; B, intermediate standing water, alkalinity 18–59; C, hard standing water, alkalinity 60–242; D, slowly running water; E, fast running water; ordinates, percentage of stations within each group which contained the leech in question.

Fig. 4 illustrates the relation between the numbers of *Erpobdella octoculata* and the numbers of *Helobdella stagnalis* in the various standing-water stations. The figures were obtained by expressing the numbers of *Erpobdella octoculata* as a percentage of the total for the two species. It is seen that *E. octoculata* is always more numerous than *Helobdella stagnalis* in soft water, and that the converse is true for hard waters of a surface area more than 5000 sq.yd. Those with a surface area less than this tend to have a higher proportion of *Erpobdella octoculata*, thus illustrating the observation made earlier that next to alkalinity, size is an important factor in leech ecology. The irregularity of the curve in the intermediate group of stations illustrates the observation that in this type of habitat particularly, factors other than alkalinity influence the balance of the fauna. It follows from the results illustrated in Fig. 4 that the ratio of *Erpobdella octoculata* to *Helobdella stagnalis* in any particular habitat is an indication of productivity, and the author has found that the rapid estimation of this ratio is a useful field technique for making a preliminary assessment of the conditions obtaining in a body of water.

The third most important factor influencing distribution is the rate of water movement. Fig. 3 shows that the distribution between standing water, slowly running water, and fast running water is markedly different for the various species. It is

probable that it is the young stages which are most affected by the current, and that unless adequate provision is made for their protection, they tend to be carried away.

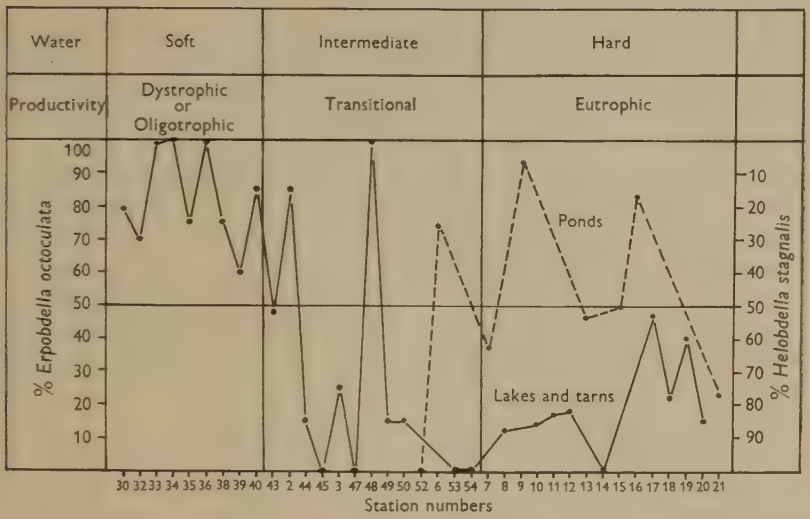

Fig. 4. The relative numbers of *Erpobdella octoculata* and *Helobdella stagnalis* in the different types of standing water. Stations arranged in order of total alkalinity. The dotted line connects stations of a surface area less than 5000 sq.yd.

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Thanks are due also to Professor A. Graham who advised on the presentation of results, and criticized the manuscript.

Fig. 2 is borrowed from a paper of Dr T. T. Macan's, with his kind permission.

SUMMARY

1. Quantitative collections of British freshwater leeches have been made in 58 localities, 29 in Berkshire and 29 in the Lake District. Six physical or chemical factors of the environment were evaluated: total alkalinity, dissolved organic matter, colour of the water, pH of the mud and of the water, and area of the water surface. Those habitats with a total alkalinity less than 18 mg $CaCO_3$/l. are classed as soft-water habitats, either oligotrophic or dystrophic, while those with a total alkalinity of more than 60 mg $CaCO_3$/l. could be regarded as hard eutrophic waters. There was a number of intermediate stations in which factors such as size, and others not evaluated, decided the nature of the habitat.

2. The most numerous leech in the soft waters was always *Erpobdella octoculata*, but greater numbers and variety of leeches were found in oligotrophic than in dystrophic waters.

3. The most numerous leech in hard, eutrophic waters was always *Helobdella stagnalis* except in the four smallest bodies of water, where *Erpobdella testacea* was more abundant.

4. In the intermediate group of stations, *Helobdella* was the more abundant in half of them, and especially in the larger basins.

5. Leeches were more abundant in the harder waters of Berkshire than in the softer waters of the Lake District, and were more numerous in habitats with more alkaline mud.

6. In running water, the fast streams with a stony bottom had *Erpobdella octoculata* as the most numerous leech; the slower streams with abundant marginal vegetation had *Helobdella* predominating. The Pang, a moderately fast river draining the chalk, yielded *Glossiphonia complanata* most abundantly.

7. Four species, *Erpobdella octoculata*, *Glossiphonia complanata*, *Theromyzon* and *Helobdella*, are found over the whole range of alkalinities. The relative abundance of *Erpobdella octoculata* and *Helobdella* is related to the total alkalinity. *Glossiphonia complanata* is numerically dominant only in the hardest-water stations of each district, and *Theromyzon*, though widely distributed, is never abundant.

8. The remaining eight species are restricted in their distribution. Three are rare: *Dina lineata*, which has been found in a temporary pond, *Hirudo medicinalis*, which is confined to small bodies of water visited by suitable vertebrate hosts, and *Batracobdella paludosa*, which prefers small ponds with an accumulation of organic matter. *Erpobdella testacea* has a much more restricted range than *E. octoculata*, but the optimum habitat has not been determined. *Haemopis sanguisuga* has been found abundantly in the Lake District, but rarely in Berkshire, while for *Glossiphonia heteroclita* the converse is true. *G. heteroclita* is also absent from running water. The two fish parasites, *Hemiclepsis* and *Piscicola*, are limnophilous and rheophilous respectively.

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* Quoted only at second hand.

THE FOOD OF THE SWIFT

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Part 1. FEEDING HABITS. By David Lack

Until now, extremely few food samples have been analysed from the common swift (*Apus apus*). The material discussed in the second and main section of this paper was obtained from two sources. In 1944, R. Vaughan caught some parent swifts at Radley near Oxford in order to ring them, and found that some of them thereupon produced the insects which they were bringing to their young. Twelve meals collected in this way were sorted and analysed by R. B. Freeman, then at the Bureau of Animal Population, Oxford, with the help of various specialists. Between 1949 and 1953, especially in 1952, a second and much larger collection was obtained mainly by D. F. Owen, with some by Dr M. M. Betts and the present writer, from a colony of swifts breeding in nesting boxes in the University Museum Tower at Oxford (described in Lack 1951, 1952). As adult swifts sometimes desert their young when caught at the nest, we employed a different method, waiting until the nestling had taken the food from the parent, then taking the nestling from the box and gently manipulating the food from its throat before it had been swallowed. This method allowed a large number of food samples to be obtained without harm to the birds. These are discussed in Part 2. My aim in this introductory section of the paper is to comment on the feeding habits of the swift.

(*a*) *Methods of searching*

The swift feeds on air-borne insects. It need scarcely be said that it does not merely fly through the air with its mouth open taking those insects which enter. It departs from such a random method in two respects. First, it seeks places where air-borne insects are abundant and avoids places where they are scarce. Secondly, it can diverge in flight to one side or the other to take insects which it sees rather off its line of flight. It cannot manœuvre so rapidly as a bird with shorter and more rounded wings, but it can turn more rapidly than its long thin wings might at first suggest. The wings are rotated like solid paddles on the extremely squat humerus. This is a different wing-action from that of passerine birds, though it is found, and carried further, in hummingbirds.

The places where swifts search for food vary with the weather. On an average fine day in summer, they often feed from 20 to 100 ft above open ground. If there is a moderate wind, a site which they particularly favour is a row of trees at right angles to the wind. Here, often accompanied by hirundines, they repeatedly fly along the belt and back again, either just above the trees or on their windward side near the top, making use of the upcurrent, which saves them energy in flight and also, perhaps, concentrates the insects from the open ground over which the wind has passed. Under such circumstances, the swifts often fly fairly close to the trees, but not so close as the

hirundines, which have more skill in manœuvre. Similarly, they do not usually feed so close to the ground as hirundines, though they make occasional swoops very low over open ground.

On extremely fine and still days, swifts may circle up to several hundred feet. Sometimes they appear to be feeding at these heights, but at other times they do not seem concerned particularly with food. Even in fine weather, of course, there are usually more insects close to the ground than higher up. Swifts have also been seen at much greater heights, even at several thousand feet (from aircraft), but this is presumably for travel, not feeding.

On wet and windy days, swifts, like hirundines, often feed low over water. In such weather terrestrial insects rarely take off and those that are in the air often descend to the ground. But some of the insects with aquatic larvae commonly emerge in rough weather. In rough weather, also, swifts often patrol a belt of trees on the windward side of a lake, in the same way that they patrol a belt of trees alongside open country in fine weather, as already mentioned. Swifts, like hirundines, are also seen feeding over water particularly at the time of their first arrival in spring.

Swifts sometimes collect in large numbers where food is specially plentiful. The great gatherings over the Cambridge Sewage Farm are famous, and I have seen similar gatherings, probably involving several thousand birds, at Minsmere in Suffolk, when midges were rising in the evening. The same has been reported in Germany (Heyder 1927). Similarly, during their autumn and spring passage through the Belgian Congo, common swifts are seen chiefly on those days when winged ants or winged termites are swarming, and of seventeen stomachs of collected birds, five contained only termites, eleven only ants and the remaining one ants with other insects (Chapin 1939, p. 458). Conversely, swifts avoid areas where their food is scarce. Thus in Europe they fly round and away from local showers or thunderstorms, and at times make large-scale movements to avoid the rain-belts of oncoming cyclones (Koskimies 1950).

Despite the evidence in the last paragraph, breeding swifts normally feed close to their nesting colonies. Indeed, if they did not do so, there would be no point in the colonies being dispersed as they are. In Oxford, for instance, small colonies of swifts, usually of less than twenty pairs, are found at intervals of perhaps $\frac{1}{4}$ to $\frac{1}{2}$ mile through the town, this spacing not being primarily due to the distribution of nesting holes. At the Museum Tower, some of the birds can almost always be seen feeding close at hand, and often most of them are there. As further evidence of this, when a sudden shower strikes the tower, quite a number of swifts come in at once for shelter, showing that they were close at hand. Because swifts feed close to their nests, the foods brought to the young probably vary with the colony. Thus the swifts breeding in Woodstock, near Oxford, regularly feed over the lake at Blenheim Park in all types of weather, whereas those at other sites feed over water chiefly in rough weather.

Further evidence that parent swifts cannot afford to travel too far from their nests for feeding is provided by the disappearance of the swift as a breeding species from central London (Fitter 1949). With the spread of houses and of smoke, insect life has become scarce in central London, and the suburbs would presumably require

such long journeys that swifts would be unable to provide enough food to raise young in the centre of the city at the present day.

These points indicate that the gatherings of swifts where food is plentiful, and their avoidance of the rain-areas of cyclones, chiefly involve individuals without parental cares. For this reason, the samples of food brought to nestling swifts, analysed in Part 2 of this paper, are probably less variable than those caught by wandering adult swifts. On the other hand, the samples are richer than those found in the true 'aero-plankton', i.e. the insects drifting through the air several hundred feet above the ground, since observations show that swifts may feed within a few feet of the ground, of trees or of water, and hence can take a greater range of air-borne insects than those characteristic of the aero-plankton. There are, incidentally, two records of swifts alighting on walls and apparently picking off insects, but this is quite exceptional (Meiklejohn 1928, Gilbert 1944).

(*b*) *Selection of prey*

While the main selection of prey occurs through choice of where to feed, swifts also exercise selection in the particular insects which they take. Thus on the evening of 29 June 1949, Dr M. M. Betts watched swifts feeding near the Museum Tower, Oxford, at a time when large beetles, later identified as the melolonthine *Amphimallus solstitialis* L., were flying over the grass and collecting round the trees. Swifts often swooped at them, sometimes catching them in the air, but then dropped them. This beetle is above the limit of size normally taken by the swift. Obviously, swifts may be expected to avoid insects which are too large, but a more subtle type of selection in regard to size is demonstrated in Part 2. Within the usual range of sizes taken by the swift, the smaller sorts of insects are taken mainly in poor weather. Small insects, of course, are usually more abundant in fine than in poor weather, but in fine weather many larger sorts are also available, and the swift evidently selects these in preference so long as they are numerous. Gibb (*in litt.*) has recorded a parallel instance in the blue tit (*Parus caeruleus*) at Wytham. Aphids are common in June and July, but the blue tit takes very few until July, since large caterpillars are still available in June.

The most remarkable evidence of visual discrimination by the flying swift is that, where swifts were regularly hunting round beehives, eight individuals were shot on different occasions and were found to contain only the stingless drones (Lacey 1910). A similar discrimination has been recorded for the alpine swift (*Apus melba*) (Hess 1927), the swallow (*Hirundo rustica*) (Stemmler-Morath 1932), and the cliff swallow (*Petrochelidon albifrons*) (Grant 1945). The last species spent much time before capturing each bee, presumably because it was avoiding the workers. Bartels (1931), however, found eleven bee stings in the throat of an alpine swift. Either this bird was exceptional, or the absence of worker bees from bird gizzards is because birds eject them from the mouth after being stung. Further study is needed.

(*c*) *Amount collected*

A few weights of meals brought to nestling swifts, with the number of insects in each, are given in Part 2. Many other meals were weighed indirectly, by weighing the nestling shortly before and immediately after the parent had fed it, as reported else-

where (Lack 1951). One parent collected 1·7 g of insects in 64 min, another 1·2 g in 47 min. The commonest weight of a meal was 1·1 or 1·2 g, the usual limits being 0·7–1·8 g, with occasional smaller ones (perhaps because the parent returned for some other reason) and very occasional larger ones up to 2·5 g. These figures include any of the parent's saliva that may have been adhering to the insects. The largest number of meals recorded as brought to a brood at Oxford in one day was 42, so that the parents probably removed about 50 g of insects from the air during the day. The average weight of a meal was similar in fine and in poor weather, but in poor weather the parents took much longer to collect it and, as already mentioned, the insects were of smaller size. It may be added that the rate at which the adult swift collects insects is far higher than that at which they are caught by a net suspended in the air to catch whatever drifts into it.

(*d*) *Daily rhythm of feeding*

C. G. Johnson (*in litt.*) kindly sent me the summarized results of his observations with nets catching aero-plankton at Cardington. In all weathers, air-borne insects were usually more abundant in the afternoon (after 1430 h) than earlier in the day. This may be compared with the feeding frequency of parent swifts in the Museum Tower, of which the hourly variations are shown in Table 1. In poor weather, the peak came

Table 1. *Feeding frequency of parent swifts at Oxford*

Hour starting (G.M.T.)	Average number of feeds per ten broods	
	Poor weather	Fine weather
0800	4·7	12·5
0900	6·9	16·1
1000	7·1	18·4
1100	10·7	19·5
1200	7·1	15·6
1300	8·8	14·8
1400	10·7	13·7
1500	10·7	12·8
1600	11·0	12·4
1700	10·5	12·3

Notes: (i) Based on 13 days of fine weather (99 brood-days watched) and 8 days of poor weather (58 brood-days watched). (ii) The average number of feeds (per brood of 2 in 10 h) was in fine weather 14 (varying from 12 to 21) and in poor weather 7 (varying from 5 to just under 10).

at 1600–1700 h, which probably coincides with the time of day when insects were most easily caught. In fine weather, however, when the birds feed more frequently, the peak came at 1100–1200 h, and there was a subsidiary peak at this hour even in poor weather. The explanation is that, when the nestling swifts have temporarily received enough food, they beg less from their parents, which are therefore less stimulated to bring food to them. As a result, in fine weather there is a decided slackening in the parents' efforts after noon. It is more difficult to interpret the similar slackening after noon in poor weather, but perhaps the parents normally take time off to find food for themselves at this time of day. It is clear from this that the feeding frequency at the nest does not give a reliable measure of the speed at which swifts are able to collect food at different times of the day.

Part 2. The food of the swift in the breeding season.

By D. F. Owen

(*a*) *Collection and identification of the meals*

This section is a summary of the food of the swift in the breeding season, as shown by meals collected from young and adult swifts at Oxford and at Radley, near Oxford. The following meals were collected: at Oxford—2 in July and August 1949, 3 in July 1950, 2 in July and August 1951, 54 in July and August 1952 and 4 in July 1953; at Radley—12 in July 1944 and 3 in July 1949. The following were responsible for collecting, sorting and identifying the meals collected in 1944 and 1952:

	1944	1952
Collector	R. Vaughan	D. F. Owen
Sorting	R. B. Freeman	D. F. Owen
Identification:		
Diptera	L. W. Grensted	L. Parmenter
Coleoptera	L. W. Grensted	P. J. Osborne and D. F. Owen (part)
Hemiptera (Aphididae)	F. H. Jacob	J. P. Doncaster
Hemiptera (other than Aphididae)	W. E. China	Not identified
Hymenoptera	Not identified	Not identified
Araneida	G. H. Locket	A. E. Le Gros

In addition, 11 meals were collected and sorted into families in 1949–51 by Dr M. M. Betts, and four meals were collected and sorted into orders in 1953 by D. F. Owen. Thus, although this part of the paper has been written by one author, it is really the combined work of all the above. Some of the orders that have been fully identified are being treated more fully in separate papers, usually by those responsible for the identifications. As each meal had to be preserved in alcohol it was a difficult task to sort and identify even the most numerous species, and although the food was not digested at all, many insects were extremely difficult to identify as they had been damaged in the bird's mouth or in the alcohol. Mainly for this reason certain orders have not been identified.

Throughout this paper the nomenclature for insects (except the Aphididae) is that of Kloet & Hincks (1945). The names of the Aphididae are from several sources, and have been used with the help of J. P. Doncaster. Locket & Millidge (1951–53) have been followed for the spiders. All species identified twenty or more times in either 1944 or 1952 are given in the Appendix. A complete list of the contents of all meals is deposited at the Edward Grey Institute of Field Ornithology, Oxford.

Extremely little has been written on the food of the swift. Madon (1938), Bacmeister (1922) and Weitnauer (1947) have examined a very small number of meals, and Moltoni (1950) investigated the stomach contents of some birds, finding that Coleoptera were most numerous, perhaps because they are slower to digest in the stomach than other insects.

The feeding methods of the swift have been discussed in Part 1, where it will be seen that the swift is entirely an aerial feeder. Thus, all insects and spiders mentioned in this paper would have been caught in the air, though as swifts sometimes feed very low, some may have been caught only a few feet above the ground or the trees.

(*b*) *The main groups represented*

Each meal consisted of a compact mass of, usually, 300–1000 insects and spiders, but some meals containing larger species had as few as 100, while others with very small insects contained as many as 1500 individuals. Hence the brood of swifts that received 42 meals in a day (Part 1) probably consumed over 20000 insects in the day. A great variety of species was represented. Thus in only 12 meals collected at Radley in 1944, 312 species were certainly identified, a figure which excludes all the Hymenoptera (fairly common) and Lepidoptera (a few), as well as many individuals of other orders which were impossible to identify. The large variety of species taken is explicable through the swift ranging over many habitats when feeding; indeed, it probably eats a greater variety of species than any other British animal.

Table 2. *The main orders represented in swift meals*

Meal	Ephemeroptera	Hemiptera	Lepidoptera	Coleoptera	Hymenoptera	Diptera	Araneida	Total
THE TWELVE MEALS FROM RADLEY, 1944								
i	—	1320	1	60	52	112	2	1547
ii	—	583	1	159	92	87	11	933
iii	—	1248	1	47	11	29	15	1351
iv	—	824	3	73	70	88	—	1058
v	—	222	5	42	102	86	5	462
vi	—	43	1	81	2	17	—	144
vii	1	66	—	274	12	35	14	402
viii	—	157	—	86	19	93	—	355
ix	—	108	2	101	29	24	—	264
x	—	569	4	259	22	77	116	1047
xi	—	683	—	6	99	89	2	879
xii	—	541	2	13	76	251	—	883
Total	1	6364	20	1201	586	988	165	9325
Species	1	87+	(−)	89+	(−)	123+	13+	312+
TWELVE MEALS FROM OXFORD*								
xiii	131	1	3	—	—	42	—	177
xiv	—	1176	—	10	9	112	5	1312
xv	—	82	—	32	8	67	5	194
xvi	—	1116	1	23	—	44	23	1207
xvii	—	191	—	41	50	115	17	414
xviii	—	132	—	2	42	68	9	253
xix	—	221	1	20	63	74	4	383
xx	—	664	—	8	27	12	5	716
xxi	—	856	—	30	58	48	24	1016
xxii	—	—	—	—	—	212	—	212
xxiii	—	43	—	—	14	463	16	536
xxiv	—	80	—	—	94	376	21	571
Total	131	4562	5	166	365	1633	129	6991

* These meals from Oxford have so far as possible been selected as representative. Meal xiii was collected in 1949, xiv–xvi in 1953, and the remainder in 1952. Also present were 1 Psocoptera, 4 Neuroptera, and meal xiii contained 18 Trichoptera.

Table 2 shows the numbers of the most numerous orders of insects and spiders in the 12 meals collected at Radley in 1944, and a sample of 12 meals from Oxford. There was considerable variation in the proportion of each order in different meals, probably due to swifts finding swarms of particular species on some days. The chief

difference between 1944 and 1952 was that aphids were very common in 1944 but scarce in 1952. Also in 1944 there were few Hemiptera other than aphids, whereas in 1952 these were common, especially in some meals collected in late July. Table 3 shows the twelve commonest species taken in 1944 and Table 4 the commonest Diptera, aphids and spiders taken in 1952.

Table 3. *The commonest species in twelve meals, Radley, 1944*

1.	*Macrosiphum avenae* (F.) (Hemipt. Aphididae)	3515
2.	*Metopolophium dirhodum* (Wlk.) (Hemipt. Aphididae)	1131
3.	*Acyrthosiphon pisum* (Harris) (Hemipt. Aphididae)	519
4.	*Meligethes aeneus* (F.) (Col. Nitidulidae)	310
5.	*Aphis fabae* (Scop.) (Hemipt. Aphididae)	268
6.	*Phyllotreta nemorum* (L.) (Col. Chrysomelidae)	226
7.	*Oscinella frit* (L.) (Dipt. Chloropidae)	167
8.	*Tachyporus hypnorum* (F.) (Col. Staphylinidae)	86
9.	*Meligethes picipes* Sturm. (Col. Nitidulidae)	63
10.	*Erigone atra* Bl. (Aran. Linyphiidae)	56
11.	*Microchrysa flavicornis* (Mg.) (Dipt. Stratiomyidae)	54
12.	*Drosophila fenestrarum* Fall. (Dipt. Drosophilidae)	50

In 1949 and 1950 Dr M. M. Betts weighed five meals soon after they had been collected. These weights are given in Table 5, together with the number of insects and spiders in each meal. It will be seen that the number of organisms in each meal was highly variable, but the weights were much less variable (for many further weights of meals see Lack 1951).

Table 4. *The commonest species* in fifty-four meals, Oxford, 1952*

1.	*Macrosiphum avenae* (F.) (Hemipt. Aphididae)	1764
2.	*Platypalpus pallidiventris* (Mg.) and/or *P. extricatus* (Collin) (Dipt. Empididae)	1439
3.	*Oscinella* spp. (Dipt. Chloropidae)	728
4.	*Erigone atra* (Bl.) (Aran. Linyphiidae)	443
5.	*Acyrthosiphon pisum* (Harris) (Hemipt. Aphididae)	392
6.	*Metolophium dirhodum* (Wlk.) (Hemipt. Aphididae)	290
7.	*Limosina* sp. (Dipt. Sphaeroceridae)	289
8.	*Lepthyphantes tenuis* (Bl.) (Aran. Linyphiidae)	238
9.	*Chrysotus* spp. (Dipt. Dolichopodidae)	216
10.	*Dilophus febrilis* (L.) (Dipt. Bibionidae)	209
11.	*Macrosiphum euphorbiae* (Thos.) (Hemipt. Aphididae)	179
12.	*Erigone dentipalpis* (Wid.) (Aran. Linyphiidae)	158

* Excluding Coleoptera and Hemiptera other than aphids

(*c*) *Size of prey*

During fine weather, when insects are often abundant in the air, swifts have a greater choice of food available, and the meals collected in such weather tended to contain the species of larger size, of approximately 5–8 mm in length. Species of smaller size, of 2–5 mm in length, were caught mainly in poor weather, when the larger species were unavailable. Very small insects of under 2 mm in length were hardly ever caught, yet these must have been present in the air in fair numbers. Thus, almost all of the aphids caught were of the larger species, and the scarcity of dipterous families such as the Cecidomyiidae was probably due to the small size of

most of the species. Really large species, of over 10 mm in length, were likewise rare; they would be difficult for a nestling swift to swallow or for an adult to store in the back of its throat.

Table 5. *Weights of meals*

	Weight (g)	Number of insects and spiders
	1·20	220
	0·80	198
	0·97	58
	1·83	808
	1·00	621
Av.	1·16	381

(*d*) *Influence of the weather*

Swifts feed their young much less often in bad weather, when food may be scarce, than in fine weather, as it takes longer to catch each meal (Lack 1951), but despite this there was not a good correlation between the weather and the type of food brought. As mentioned in the previous section, there was a tendency for larger insects to be caught on fine days and smaller insects on dull days, but this did not always hold—notably in 1944 when aphids were unusually abundant in fine weather and easily caught. As each meal is of roughly the same size, the number of insects depends on their size. Seven meals collected in very fine weather contained an average of 217 per meal, whereas four meals collected in dull windy weather contained an average of 838. If it takes a swift as long to catch a small as a large insect, a meal containing many small species would take considerably longer to catch than a meal containing fewer insects, and evidently the presence of small insects in the meals is a sign that larger species are unavailable.

As shown in Part 1, swifts tend to feed over water in bad weather, but only one meal collected in such weather contained a large number of aquatic species (mainly Ephemeroptera), though others, such as those containing many *Helophorus* spp., could have been caught partly over water. Weitnauer (1947) gives another record of a swift meal containing a large number of Ephemeroptera.

In 1952, and particularly in 1953, aphids were more numerous in the meals on cooler days when the temperature was between 62 and 66° F, than on hot sunny days, when perhaps other larger insects were more available. Spiders, which apparently dislike wind (Freeman 1946), were often caught on windy days, but they need not have been very abundant in the air, as the swifts may have had to search hard for them. Sun-loving insects, such as the Syrphidae and many of the Curculionidae, were more numerous in the meals on fine than on dull days.

Johnson (1952) has pointed out that other factors besides weather are important in determining the numbers of insects, particularly aphids, in the air. In aphids the rapid changes in the number of alatae on the plants caused by moulting, accumulation before flight and depletion by flight, might obscure any changes due to the weather, and a high population on the plants might mean large numbers in the air, even if the weather is relatively unsuitable for flight. Other authors were aware of, but did not

stress, the importance of changing numbers on the ground when attempting to correlate aerial trapping records with the weather. In view of this it is perhaps not surprising that the correlation between the weather and the food of the swift is not always good.

(*e*) *The main families and species in the meals*

HEMIPTERA. In 1944 all Hemiptera were identified, in 1952 only the Aphididae, while in 1949–51 the Hemiptera were sorted into families, but only a few were identified down to species. In 1944, 6196 aphids were found in 12 meals, an average of 516 per meal. In 1952, on the other hand, there were only 3409 in 54 meals, an average of 63 per meal (only 19 of the meals contained any aphids). In 1953 there were 2879 in four meals. The proportions of the various species in 1944 and 1952 were similar. *Macrosiphum avenae* (F.), a pest of grain, was the commonest species, and was found in all but one of the meals that contained aphids. As shown in Table 3 this species was by far the commonest insect caught by the swifts in 1944, and comprised about 38% of the total food. There were 1116 *M. avenae* in one meal (meal i in Table 2). Other species of economic importance that were common in both years were *Metopolophium dirhodum* (Wlk.), *Rhopalosiphum maidis* (Fitch) and *R. insertum* (Wlk.) (grain), *Acyrthosiphon pisum* (Harris) (peas), *Aphis fabae* Scop. and related species (beans) and *Macrosiphum euphorbiae* (Thos.) (potatoes).

Of Hemiptera other than Aphididae, fourteen families were represented in the meals collected in 1944 and 1949–51, the numbers of the commonest families, including the Aphididae, being given in Table 6. In 1952 there were 3402 Hemiptera other than aphids and in 1953 there were 86, but none of these has been identified.

Table 6. *The commonest families of Hemiptera, 1944–51*

Meals were collected as follows: Radley—12 in 1944 and 3 in 1949; Oxford—2 in 1949, 3 in 1950 and 3 in 1951; the 29 Cixiidae were all in one meal.

	Number of individuals	
	Radley	Oxford
Aphididae	6394	183
Jassidae	25	123
Delphacidae	15	105
Chermidae	62	17
Typhlocybidae	65	4
Miridae	28	11
Cercopidae	1	36
Cixiidae	—	29
Nabidae	8	9

COLEOPTERA. All the beetles collected in the meals in 1944 were, so far as possible, identified. Nineteen families were represented, the most numerous being the Nitidulidae (33% of total), Chrysomelidae (25%), Staphylinidae (15%) and Curculionidae (13%). The commonest species were *Meligethes aeneus* (F.) (26% of all beetles taken) and *Phyllotreta nemorum* (L.) (18%). As shown in Table 3 these were the fourth and sixth commonest species, respectively, caught by swifts in 1944. Only the most numerous species caught in 1952 have been identified. In four meals collected on

three days there were many *Helophorus* spp., whereas only two were recorded in 1944 (single specimens in two meals). Likewise *Sitona lineatus* L., a pest of beans, was not recorded in 1944, but was numerous on some days in 1952; in eleven meals containing 1091 beetles, there were 341 of this species. In 1952, as in 1944, *Phyllotreta* spp. were common, but whereas in 1944 the commonest species was *P. nemorum* (L.), in 1952 it was *P. atra* (F.).

DIPTERA. In 1944 there were 988 Diptera in 12 meals, an average of 84 per meal, and in 1952 there were 4047 in 54 meals, an average of 75 per meal. About 5000 Diptera, representing 38 families, have been identified from the meals collected in 1944 and 1952, the commonest families being the Empididae (30% of total), Chloropidae (20%), and Sphaeroceridae (7%). The high proportion of Empididae, especially in 1952, was due to the abundance of *Platypalpus pallidiventris* (Mg.) and *P. extricatus* (Collin) (Table 4), which together comprised about 29% of the Diptera. *Oscinella* spp., mainly *O. frit* (L.), (Chloropidae) were common and comprised 19% of the Diptera. The rather high proportion of Bibionidae (Appendix) was due largely to 209 *Dilophus febrilis* (L.) in one meal (Meal xxii in Table 2), otherwise this family was little represented in the diet of the swift. The scarcity of crepuscular Diptera, such as the Chironomidae and many of the Tipulidae, was probably because most meals were collected during the middle hours of the day. Two meals collected late in the day did contain considerable numbers of Chironomidae.

HYMENOPTERA. Almost all the Hymenoptera were small species (Ichneumonidae, Braconidae), but there were a few large ichneumons and one meal contained many flying ants, probably the result of the swift finding a local swarm. There were no bees or large wasps.

ARANEIDA. In 1952, 46, and in 1944, 7, meals contained spiders, a total of 1260 and 165 individuals respectively. Spiders were relatively unimportant in the diet of the swift, and except on one day in 1952, they comprised less than 5% of a meal. Most belonged to the Linyphiidae and in this family all those identified were adults, except for 11 immature *Lepthyphantes tenuis* (Bl.) and 17 immature *Erigone* spp. Other families (Thomisidae, Lycosidae, Theridiidae, Tetragnathidae and Argiopidae) were unimportant, each being represented by only a few immature specimens, the adults being too large to be found in the air. In both years *Erigone atra* (Bl.) and *E. dentipalpis* (Wid.) were the commonest species, and together comprised 48% of all spiders taken. The proportion of other species was similar in both years, the commonest being *Lepthyphantes tenuis* (Bl.), *Dicybium nigrum* (Bl.) and *Oedothorax fuscus* (Bl.). The chief difference between the years was that in 1952 only two *Meioneta rurestris* (C.L. Koch) were found, whereas in 1944 this species comprised 12% of all spiders caught.

OTHER ORDERS. In each year Ephemeroptera, Trichoptera, Plecoptera, Neuroptera, Odonata and Lepidoptera were usually represented by only a few specimens. On a rough day in 1952, however, one meal contained three Odonata (one *Coenagrion pulchellum* van der Linden and two *C. puellum* L.). The Lepidoptera were usually of small size, but there were occasional Hepialidae and Caradrinidae in some meals.

(*f*) *Daily variation in the numbers of some species*

Table 7 shows the numbers of some species on different days in 1944 and 1952. There was a marked tendency for certain species to be confined to particular days, probably due to their changing numbers in the air caused by emergence and death, and perhaps also to the weather. Thus, in 1944 *Microchrysa flavicornis* (Mg.), *Drosophila fenestrarum* Fall., *Meligethes aeneus* (F.), *Lema melanopa* (L.), *Phyllotreta*

Table 7. *Daily variation in the numbers of some species*

Date—July 1944 ...	13	14	15	16	17	19	22
Number of meals examined ...	1	1	2	1	3	2	2
Microchrysa flavicornis (Mg.) (Dipt.)	—	—	—	—	—	3	51
Platypalpus pallidiventris (Mg.) (Dipt.)	7	4	5	3	8	9	7
Drosophila fenestrarum Fall. (Dipt.)	—	—	3	2	1	—	44
Oscinella frit (L.) (Dipt.)	34	9	24	16	53	42	9
Tachyporus chrysomelinus (L.) (Col.)	1	22	8	3	4	10	—
T. hypnorum (F.) (Col.)	1	23	14	5	8	35	—
Meligethes aeneus (F.) (Col.)	4	31	19	2	33	221	—
Adalia decempunctata (L.) (Col.)	—	2	—	—	44	2	—
Lema melanopa (L.) (Col.)	—	—	—	24	1	—	—
Phyllotreta nemorum (L.) (Col.)	—	1	1	—	209	15	—
Phytonomus nigrirostris (F.) (Col.)	—	4	—	—	25	4	—
Macrosiphum avenae (F.) (Hemipt.)	91	290	775	465	167	175	1552
Acyrthosiphon pisum (Harris) (Hemipt.)	77	98	89	104	47	16	88
Metopolophium dirhodum (Wlk.) (Hemipt.)	234	155	476	137	16	28	85
Aphis fabae (Scop.) (Hemipt.)	55	45	77	29	11	7	44
Erigone atra Bl. (Aran.)	—	3	2	1	1	48	1

Date—July 1952 ...	2	12	14	15	17	18	19	21	25	29	31
Number of meals examined ...	4	10	6	8	10	3	4	3	2	1	1
Sciara spp. (Dipt.)	13	85	33	45	20	3	—	—	—	—	—
Odontomyia viridula (F.) (Dipt.)	57	—	2	—	—	—	—	—	—	—	—
Platypalpus pallidiventris (Mg.) and/or *P. extricatus* (Collin) (Dipt.)	—	1131	81	120	49	45	5	—	2	—	1
Oscinella spp. (Dipt.)	6	281	196	101	57	22	2	2	11	—	19
Limosina spp. (Dipt.)	8	132	48	52	35	5	1	3	1	—	—
Sepsis spp. (Dipt.)	2	16	15	25	17	3	1	2	1	—	2
Chrysotus spp. (Dipt.)	10	118	30	38	8	6	1	3	—	—	—
Acyrthosiphon pisum (Harris) (Hemipt.)	36	95	82	—	179	—	—	—	—	—	—
Macrosiphum euphorbiae (Thos.) (Hemipt.)	1	71	40	—	67	—	—	—	—	—	—
M. avenae (F.) (Hemipt.)	28	300	237	—	1216	—	—	—	—	—	—
Metopolophium dirhodum (Wlk.) (Hemipt.)	43	83	57	—	107	—	—	—	—	—	—
Hyperomyzus lactucae (L.) (Hemipt.)	23	4	1	—	4	—	—	—	—	—	—
Erigone dentipalpis (Wid.) (Aran.)	7	11	17	98	16	7	—	—	2	—	—
E. atra (Bl.) (Aran.)	7	38	42	245	65	34	1	3	8	—	—
Lepthyphantes tenuis (Bl.) (Aran.)	—	27	9	168	21	6	—	—	4	1	2

From 19 July onwards most of the meals contained a large number of Hemiptera other than aphids, which have not been identified.

nemorum (L.), *Adalia decempunctata* (L.), *Phytonomus nigrirostris* (F.) and *Erigone atra* (Bl.) were largely confined to single days. When more than one meal was obtained on the same day the same species were usually, but not always, numerous. Other species, however, such as *Platypalpus pallidiventris* (Mg.), *Oscinella frit* (L.), *Tachyporus chrysomelinus* (L.) and *T. hypnorum* (F.), were common on most days, though in these species also, more were found on some days than on others. The four common aphids, *Macrosiphum avenae* (F.), *Acyrthosiphon pisum* (Harris), *Metopolophium*

dirhodum (Wlk.) and *Aphis fabae* (Scop.), were well represented in all the meals, suggesting that they were common in the air throughout the period when the meals were obtained. The results were similar in 1952 when a larger number of meals was collected on each day. Thus, in four meals collected on 2 July there were no *Platypalpus* spp., but in 10 meals collected on 12 July there were 1131, after which their numbers decreased until 19 July, and from then on few were taken. Similarly, the numbers of *Sciara* spp., *Oscinella* spp., *Limosina* spp. and *Chrysotus* spp. were low on 2 July, high on 12 July and subsequently, until 19 July. The three species of spiders in Table 7 all reached peak numbers on 15 July, as did most other spiders. Some insects, such as *Dilophus febrilis* (L.), were common in only one meal, and many, such as *Odontomyia viridula* (F.), were common on only one day. Swifts apparently catch those insects that are available, and the changing numbers of different species in the meals probably reflect changes in the composition of the aerial fauna. Some species, common for only a limited period, were taken in large numbers, in view of which it is not worth attempting a more detailed comparison of the different years, as such comparisons are so greatly influenced by the dates on which the meals were collected and the time of hatching of the species involved.

(*g*) *Comparison with trapping records*

In this country the most complete study of the insect population in the air is by J. A. Freeman (1945). He found that the total density of insects rose from March to June, was low during July and part of August, rose again towards the end of August to a peak in September and fell off to the end of October. Unfortunately he did not separate his results for different families and species according to the time of year, but his records for the whole of the summer may be compared with the swift meals.

Taking the orders of insects and the spiders in the same order as before, Hemiptera were the second most numerous, and in the upper air they were by far the commonest insects. The commonest species at all levels was an aphid *Brevicoryne brassicae* (L.). Few, however, were caught by the swifts. (The large number trapped was probably due to a cabbage field nearby.) The most numerous aphids taken by the swift in 1944 and 1952 (Tables 3 and 4) were not among the twenty commonest species in Freeman's samples. Other aerial trapping records show that aphids reach a peak in July, though the actual numbers may vary considerably from year to year (Johnson & Eastop 1951, Broadbent & Doncaster 1949). In July 1944, when large numbers of aphids were caught by the swifts at Radley, Broadbent & Doncaster found correspondingly that aphids were exceptionally abundant at twelve places in England and Scotland, the numbers being greater than in five other years. They suggested that the reason was the dry weather, but in July 1952, the driest July at Oxford for 21 years, aphids were relatively unimportant in the diet of the swift. (This does not necessarily mean that aphids were sparse, as already mentioned.)

Freeman found that the commonest families of Coleoptera in the air were the Staphylinidae, Lathridiidae, Chrysomelidae and Curculionidae, the last named being mainly confined to June. The commonest families caught by swifts in 1944, in order of numbers taken, were the Nitidulidae, Chrysomelidae, Staphylinidae and Curcu-

lionidae. The most numerous species of beetles in Freeman's samples were *Corticarina fuscula* (Gyll.) and *Enicmus transversus* (Ol.), the twelfth and twentieth commonest of all insects, whereas in 1944 the most numerous species caught by the swifts were *Meligethes aeneus* (F.) and *Phyllotreta nemorum* (L.), the fourth and sixth commonest of all insects.

Diptera were the most abundant order in the aerial samples made by Freeman, comprising 37% of all insects taken during the summer. The most numerous families were the Sciaridae, Chloropidae, Sphaeroceridae and Cecidomyiidae, and the most numerous families caught by the swifts, in order of numbers taken, were the Empididae, Chloropidae and Sphaeroceridae. Freeman found that *Oscinella* spp. were the most frequently trapped Diptera and the fourth commonest of all insects. In 1944 they formed a large proportion of the Diptera caught by the swifts and were the seventh most numerous insect. *Platypalpus* spp., which were the commonest Diptera caught by the swifts in 1952, were not among the 20 most common species in Freeman's samples.

Hymenoptera were the fourth commonest order in the 1944 meals and the third commonest in Freeman's samples. Other orders fairly well represented in the traps, but rare in swift meals, were the Thysanoptera and Psocoptera (both very small). Ephemeroptera, Lepidoptera and Odonata were rarely trapped and were only occasionally found in swift meals.

Most of the species of spiders caught by the swifts have figured prominently in aerial samples, particularly the two *Erigone* spp. (Bristowe 1929, 1939–41, Smith 1904, Freeman 1946). Some authors have stated that the peak movements of the Linyphiidae, which is by far the commonest family found in the air, occur in the cooler months of the year, not in mid-summer. However, the records from the swift meals show that there must also be considerable numbers of spiders in the air in July.

Thus, there are some marked similarities and also some marked differences in the species, families and orders trapped and those caught by the swifts. Many of the differences might be explained by the time of year, the local environment and selection of certain species by the swifts.

(*h*) *Where do swifts feed?*

It was extremely difficult to tell from the meals where the adult swifts had been feeding, as comparatively little is known about the distribution of most species of insects in the air. Also many insects, perhaps the majority, probably range over a wide variety of habitats when airborne, and for these reasons it is hard to form any definite conclusions. Freeman (1945) studied the insect population from ground level to 277 ft and found that in all orders numbers decreased with increasing height; thus swifts should catch their food more easily by flying low than flying high. That swifts do feed fairly low is shown in Part 1, and this is largely confirmed by the records of insects in the meals, as many of the species might be expected to be concentrated near the ground. Almost all the meals collected indicate that the birds had been hunting over low-lying agricultural country, especially at Radley where the large proportion of grain aphids suggests feeding over fields. This type of habitat is a feature of the countryside round Oxford, but many of the commonest species caught could

also have been in the air over the city of Oxford itself. (In fine weather swifts breeding in the Museum Tower often feed close to their nests.) In bad weather there was little evidence from the meals that the swifts changed their feeding places, but rather that they searched harder for each meal. As already mentioned only one meal, collected during bad weather at Oxford in August 1949, contained a large number of aquatic insects (meal xiii in Table 2), indicating that the swift had been feeding over water.

(*i*) *Distasteful insects*

There was no evidence from the meals that the adult swifts avoided insects with warning or mimetic coloration. Many yellow and black syrphids were taken, but perhaps swifts approaching them at speed and at approximately the same level in the air, would not see the colours. Bees and larger wasps were not found in the meals, but these are much larger than the average size of insect that the swift catches. Carpenter (1938) gives a record of seven to eight swifts catching considerable numbers of a presumably warningly coloured moth *Parasemia plantaginis* (L.), on a moor in Lancashire. The weather at the time was fine and other species of Lepidoptera were ignored.

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SUMMARY

1. Swifts feed on air-borne insects, but take more varied foods than those in the true aeroplankton, since they often feed close to the ground, to trees or to open water.

2. They seek out places where air-borne insects are abundant; this varies with the weather.

3. Eighty-one food balls brought by parent birds to their young were analysed. Homoptera and Diptera were specially common, while Hymenoptera, Coleoptera and Araneida were well represented. A huge variety of species was taken, indeed the swift probably eats more species than any other British animal. The specific content of the meals differed greatly. Some contained a large number of one species.

4. Insects of more than 10 mm and less than 2 mm were rarely taken. In fine weather, those of 5–8 mm were usually selected in preference to those of 2–5 mm, but the latter were taken in large numbers in poor weather, when larger sorts were scarce.

5. There was no evidence from the meals that swifts avoided mimetic or warningly coloured insects; syrphids were quite common. But a published record shows that swifts preying on hive-bees took only the drones.

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APPENDIX

The commonest species identified

	Radley, 1944 (12 meals)	Oxford, 1952 (54 meals)
HEMIPTERA		
Aphididae		
Acyrthosiphon pisum (Harris)	519	392
Aphis fabae Scop.	268	119
A. ilicis Kltb.	28	—
Cavariella pastinacae (L.)	—	28
Dactynotus sonchi (L.)	—	23
D. jaceae (L.)	25	9
Drepanosiphum plantanoides (Schr.)	2	39
Euceraphis nigritarsis (v. Heyd.)	11	63
Hyalopterus pruni (Geoffr.)	35	83
Hyperomyzus lactucae (L.)	30	32
Macrosiphum euphorbiae (Thos.)	7	179
M. avenae (F.)	3515	1764
Megoura viciae Buckt.	4	37
Metopolophium dirhodum (Wlk.)	1131	290
Myzus persicae (Sulz.)	44	24
Rhopalosiphum insertum (Wlk.)	31	98
R. maidis (Fitch.)	—	26
Thecabius affinis (Kltb.)	4	31
COLEOPTERA		
Hydrophilidae		
Helophorus spp.	2	97 (in 11 meals)
Staphylinidae		
Tachyporus chrysomelinus (L.)	48	?
T. hypnorum (F.)	86	?
Tachyporus spp.	33	?
Nitidulidae		
Meligethes aeneus (F.)	310	?
M. picipes Sturm.	63	?
Mycetophagidae		
Typhoea stercorea (L.)	27	?
Coccinellidae		
Adalia decempunctata (L.)	48	5 (in 11 meals)
Chrysomelidae		
Lema melanopa (L.)	25	?
Phyllotreta nemorum (L.)	226	128 (in 11 meals)
P. atra (F.)	3	462 (in 11 meals)
Curculionidae		
Sitona puncticollis Steph.	31	?
S. lineatus L.	—	341 (in 11 meals)
Phytonomus nigrirostris (F.)	33	?
Stenocarus fuliginosus (Marsh)	49	?
DIPTERA		
Bibionidae		
Dilophus febrilis (L.)	—	209
Mycetophilidae		
Sciara spp.	66	199
Stratiomyidae		
Microchrysa polita (L.)	2	40
M. flavicornis (Mg.)	54	—
Odontomyia viridula (F.)	—	59
Tabanidae		
Haematopota pluvialis (L.)	—	27

	Radley, 1944 (12 meals)	Oxford, 1952 (54 meals)
DIPTERA (*cont.*)		
Empididae		
Platypalpus pallidiventris (Mg.)	43	40
P. extricatus (Collin) or *P. pallidiventris*	—	1399
Platypalpus spp.	7	69
Dolichopodidae		
Chrysotus gramineus (Fall.)	—	67
Chrysotus spp.	1	149
Lonchopteridae		
Lonchoptera lutea Panz.	5	23
Phoridae		
Megaselia spp.	15	38
Syrphidae		
Melanostoma scalare (F.)	2	20
Platycheirus clypeatus (Mg.)	—	21
Metasyrphus consisto (Harris)	15	20
Sepsidae		
Sepsis spp.	28	84
Chamaemyiidae		
Chamaemyia aridella (Fall.)	25	—
Ephydridae		
Hydropta griseola (Fall.)	—	32
Sphaeroceridae		
Trichiapsis equina (Fall.)	8	24
Limosina spp.	25	289
Drosophilidae		
Drosophila fenestrarum Fall.	50	—
Drosophila spp.	54	31
Agromyzidae		
Phytomyza spp.	27	47
Chloropidae		
Oscinella frit (L.)	167	—
Oscinella spp.	60	728
ARANEIDA		
Linyphiidae		
Savignia frontata (Bl.)	—	60
Erigone dentipalpis (Wid.)	26	158
E. atra (Bl.)	56	443
Oedothorax fuscus (Bl.)	—	39
Bathyphantes gracilis (Bl.)	4	95
Lephthyphantes tenuis (Bl.)	25	227
Meioneta rurestris (C. L. Koch)	20	2

SOME EXPERIMENTS ON THE VERTICAL MIGRATION OF ZOOPLANKTON

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(With 14 Figures in the Text)

Hardy & Paton (1947) have described two forms of apparatus with which to study the vertical migration of plankton animals; their intention was to carry out experiments under conditions as natural as possible. In their paper were published results for marine copepods; Paton had also used the instruments on freshwater plankton animals in Windermere, but before he was able to analyse the results, he was killed in action over Malta. After the war, Professor Hardy kindly allowed me to work up the results of Paton's freshwater experiments. One point that emerged from the analysis was that there was a difference in behaviour between animals caught from 15 m to the surface and those caught from 30 m to the surface. Experiments carried out by me in Windermere in 1947 were intended to investigate this difference. A night series was also completed, comparable to one that Paton carried out in 1939. Experiments were also carried out in the North Sea from the Fisheries Research Vessel *Sir Lancelot*; these consisted of two night series, one at 10 m and the other at 70 m.

APPARATUS

The two forms of apparatus used were the 'Double Standard' apparatus and the 'Long Tube'. The first (Fig. 1) consists of two wide glass tubes (int. diam. 3 in.), closed at the top with glass disks and at the bottom with taps; the two tubes are slung vertically side by side in a metal frame. They are 1 m in length and each is divided half way down by a trapdoor; the two trapdoors are operated from the outside by a centrally placed mechanism on the frame. The apparatus is lowered on a suspending wire to the depth of observation and a messenger operates the central mechanism, in order to open the trapdoors; when the experiment is over, a second messenger closes the doors. The four sections in the machine are named A, B, α and β.

The 'Long Tube' (Fig. 2) consists of one wide glass tube (int. diam. 3 in.), of seven sections (A, B, C, D, E, F, G, the last being the bottom section); the whole tube is $13\frac{1}{2}$ ft long. The sections are connected to each other by short wide rubber tubes, secured by brass ring clamps to the glass tubes of the sections. Each section is linked to a supporting cable by thumbscrew clamps on metal connecting pieces. The trapdoors, which are in these connecting pieces, are operated by means of a weighted line that is connected to each, externally. The tube was built up in sections on the supporting cable as it was lowered gradually into the water. Both forms of apparatus were used at a number of depths, the double standard apparatus down to 70 m and the long tube down to 20 m.

METHOD

Animals were caught between 0800 and 0900 h G.M.T., in Windermere with a small conical closing net (180 meshes/linear inch), and in the North Sea with a Clarke-Bumpus sampler (60 meshes/in.). The animals were kept, thinly dispersed, in semi-

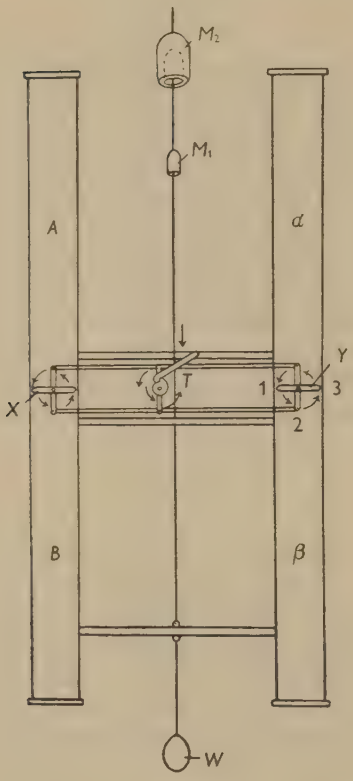

Fig. 1

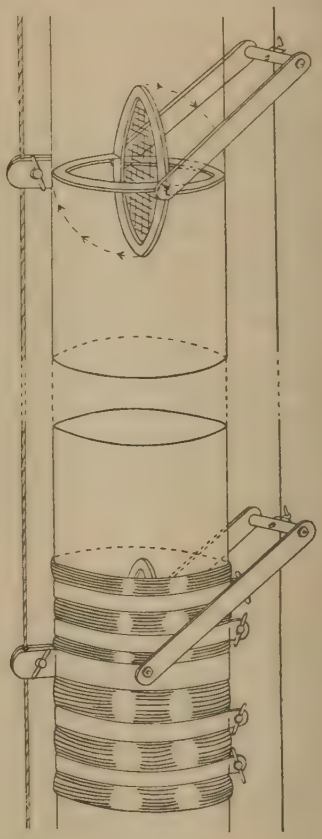

Fig. 2

Fig. 1. A simplified diagram of the double standard apparatus. The trapdoors, X and Y, are operated by the central trip mechanism, T. The first messenger, M_1, opens the trapdoors and the second messenger, M_2, closes them. The successive positions of the trapdoors are shown at Y; a weight W stabilizes the apparatus.

Fig. 2. One section of the long tube, showing (above) the internal arrangement and (below) the external arrangement of the trapdoors, with the rubber and brass rings connecting the sections. The supporting cable is shown on the left and the weighted hand line for opening and closing the trapdoors is shown on the right.

darkness in 7 lb jars. The lake water, or sea water, was filtered through fine silk to remove the animals and some of the plants. When the double standard apparatus was used, the experimental animals were siphoned from the centre of the 7 lb jar to the β section. The β and B sections were filled up with water to the trapdoors, which were

then closed; the A section was filled with animals and water and the α section was filled with water only. The glass disks on the top of each tube were then screwed down, making sure that no air bubbles were trapped. The whole operation was completed in semi-darkness. The apparatus was then covered with a black cloth, lowered over the side and the black cloth was removed. This procedure was carried out in order to minimize the effect of strong daylight on the behaviour of the animals. The machine was then lowered to the depth at which the experiment was to be carried out.

Using the long tube, the procedure could not be carried out in the same way. Animals were siphoned from the centre of the 7 lb jar (which was kept in semi-darkness) into the appropriate section of the tube, when it was in the lake and clamped on to the cable. This achieved the same end.

In 1939 Paton made light measurements at the surface and at the experimental depths with a Bernheim photocell and a Cambridge Unipivot galvanometer (Ullyott 1934). A resistance (250 Ω) was used for the surface and shallow readings. In 1947 light measurements were made with Weston photocells and a Cambridge Unipivot galvanometer. In 1948 in the North Sea Weston photocells, a Tinsley galvanometer and an attenuator were used. The galvanometers were all low resistance instruments. After the war Paton's photocell was no longer accessible; the photocell used in 1948 was not calibrated until late in 1949. Hence, the calibration values of this cell would not necessarily be applicable to the 1948 series. Measurements of light intensity are only used within experimental series and are expressed as the percentage of the reading given on the deck cell. An opal disk was used over each cell and the deck cell was always covered with water.

In 1939 temperature readings were made at the same time as each experimental observation. As these readings could not be correlated with the experimental results, temperature readings were only taken in 1947 when the long tube was set across a thermocline. In this instance a thermistor resistance thermometer was used.

When observations were made, the state of weather and state of sea (or lake surface) were recorded.

TREATMENT OF RESULTS

The following animals were found in Windermere, but sometimes only in sufficient numbers to be used for a few experiments:

Copepoda: *Diaptomus gracilis* Sars; *Cyclops strenuus* Fischer.

Cladocera: *Daphnia hyalina* Leydig; *Leptodora kindti* Focke; *Bythotrephes longimanus* Leydig.

In the North Sea the following animals were used:

Copepoda: *Calanus finmarchicus* Gunner; *Pseudocalanus elongatus* Boeck; *Temora longicornis* Müller.

In all experiments with the double standard apparatus, the plankton was put into sections A and β (Fig. 1) at the beginning of each experiment, i.e. in the top half of one tube and in the bottom half of the other. During the experiment, after the trap-doors were opened, animals were free to move up to α or down to B; when the experiment was over, the traps were closed and the animals in each section were killed and preserved. Each sample was analysed for every organism being examined;

those species that occurred in sufficient numbers were determined for sex and developmental stages. The percentages of animals that moved from one section to another have been based wherever possible on numbers greater than 100. In no case have numbers less than 25 been used.

In the following treatment, A means the number of animals found in section A, expressed as a percentage of those introduced on that side of the apparatus. The relation between numbers in section A and section B is expressed as $A = 100 - B$; similarly, $\alpha = 100 - \beta$. The percentage value, α is a measure of upward aggregation and the percentage value, B, is a measure of downward aggregation.

The mean upward or downward aggregation is represented by the difference of the value of $(A+\alpha)/2$ from 50%. Had there been no movement from section A or from section β, $(A+\alpha)/2$ would have been 50%, and again had any equal percentage moved both up and down, the same value would have been obtained. When considering the mean movement up or down the deviation from A or α is $A-\alpha$ and that from $(A+\alpha)/2$ is $(A-\alpha)/2$. If experiments were carried out for too short a duration, $A > \alpha$ and the estimate of deviation would be much too high; in fact $A > \alpha$ in 71 experiments, and in a further 71 $A < \alpha$.

The estimate of variance of $(A+\alpha)/2$ used was $\frac{1}{n}\Sigma\left(\frac{A-\alpha}{2}\right)^2$, where n is the number of experiments on each copepodite stage, sex or species of an animal, in any one experimental series. From this estimate, a standard deviation was extracted and, for any one experimental series, an error of twice this standard deviation was assigned to each observation. Thus, it is possible to see from the graphs in Figs. 3–8 whether any observation is significantly different from 50% or from any other observation. On some of the graphs it will be seen that some estimates of error reach the abscissae; the meaning of this is that there is a certain probability of the observation being 0 or 100%.

A is consistently greater than α in some experimental series, e.g. experiments 26–38, the deep water series (see Table 3 Appendix). Furthermore, there are marked regressions of $(A-\alpha)/2$ for stage IV on $(A-\alpha)/2$ for stage V, for these experiments. The variances were evidently biased in some systematic way as the animals tended to remain where they were put. If this is so, then a component of variance would be attributable to this inertia. Hence, it is probable that the variances assigned to the observations in these experiments are much larger than they should be, were they entirely attributable to random error.

RESULTS

(*a*) *Double standard, daylight, (Fig. 3); tendency to aggregation at different depths*

Five sets of experiments (1–3, 4–9, 26–29, 30–34, 35–38) were made in full daylight in July between 0800 and 1600 h G.M.T. The plankton for the experiments was taken in full daylight from either a shallow depth range (0–30 m) or from a greater depth range (30–50 m); the first two sets (1–9) were carried out on plankton of shallow origin, the middle set (26–29) on plankton of mixed origin (0–50 m) and the last two sets (30–38) on plankton of deep origin in each set. Experiments were made at a number

of depths from the surface down to 20 m, so plankton of the same origin was subjected to simultaneous variation in depth and in light intensity. There was some variation in light intensity from one day to another and this caused an anomaly in experiments 26–29, which were not made on the same day; in that set, the light intensity at 15 m was greater than that at 10 m, a difference of which account will be taken later.

Table 1. *Experiments carried out*

Expts.	Plankton from (m)	
	Windermere 1939: North Basin	
1–3	30– 0	Expts. at 20, 1 and 10 m. D.S., daylight
4–8	15– 0	Expts. at 15, 15, 10, 5 and 1 m. D.S., daylight
9	10– 0	Expt. at 5 m. D.S., daylight
10–12	40– 0	Expts. at 0 m. Long tube; plankton put in sections G, D and A
13	40– 0	Expts. at 5 m. Long tube; plankton put in section G
14–20	5– 0	Expts. at 5 m, except expt. 16, which was at 1 m. Night series, D.S.
	Windermere 1947: Centre Buoy, North Basin	
21–25	10– 0	Expts. at 1, 5, 10, 15 and 20 m. D.S., daylight. (Numbers insufficient)
26–29	40–30	Expts. at 1, 5, 10 and 15 m. D.S., daylight
30–34	50–40	Expts. at 1, 5, 10, 15 and 20 m. D.S., daylight
35–38	50– 0	Expts. at 1, 5, 10 and 15 m. D.S., daylight
39–46	40– 0	Expts. at 0 m. Long tube; plankton in G. Duration 30, 1, 2, 3, 4, 5, 10 and 20 min. Daylight
47	40– 0	As 39–46, duration 15 min. Long tube. Daylight (Numbers insufficient)
48–49	40– 0	Expts. at 0 m. Long tube; plankton in D and A. Daylight
50–52	40– 0	Expts. at 10 m. Long tube; plankton in G and D. Daylight
53	40– 0	Expts. at 20 m. Long tube; plankton in G
54–60	50– 0	Expts. at 1 m. Night series. D.S.
	North Sea 1948: 35 miles south-east of Shields	
61–66	70–50	Expts. at 70 m. Day and night series. D.S.
67–71	70–50	Expts. at 10 m. Night series. D.S.

In experiments on plankton of shallow origin (1–9), *Diaptomus* aggregated upwards, whereas in experiments on plankton of deep origin (26–34), the same species aggregated downwards. The four experiments on plankton of mixed origin (35–38) yielded mixed results, *Diaptomus* aggregating neither upwards nor downwards. We may therefore make a distinction between *Diaptomus* of different depth origin. In *Diaptomus* upward and downward aggregation were shown by animals of different origin. Both forms of aggregation were shown by *Cyclops strenuus*, an animal of one origin (experiments 1–3; 0–30 m). At 1 m *Cyclops* aggregated downwards and at 20 m it aggregated upwards; at 10 m neither upward nor downward aggregation took place. Aggregation by *Diaptomus*, in experiments on plankton of both deep and shallow origin, shows a consistent pattern at the different depths. This pattern is a change in aggregation with depth and not a change in position as in normal vertical-migration diagrams. Examining the shallow-origin experiments 1–3 in detail, it will appear from Fig. 3 that there is significant upward aggregation at 10 m only and none at 1 and 20 m.

Again in experiments 4–9 there is significant upward aggregation at 1 and 5 m but not at 10 and 15 m. It is worth noting that where the depth of upward aggregation was at 5 m the depth of plankton origin was 0–15 m and that where the depth of upward aggregation was at 10 m the depth of plankton origin was 0–30 m.

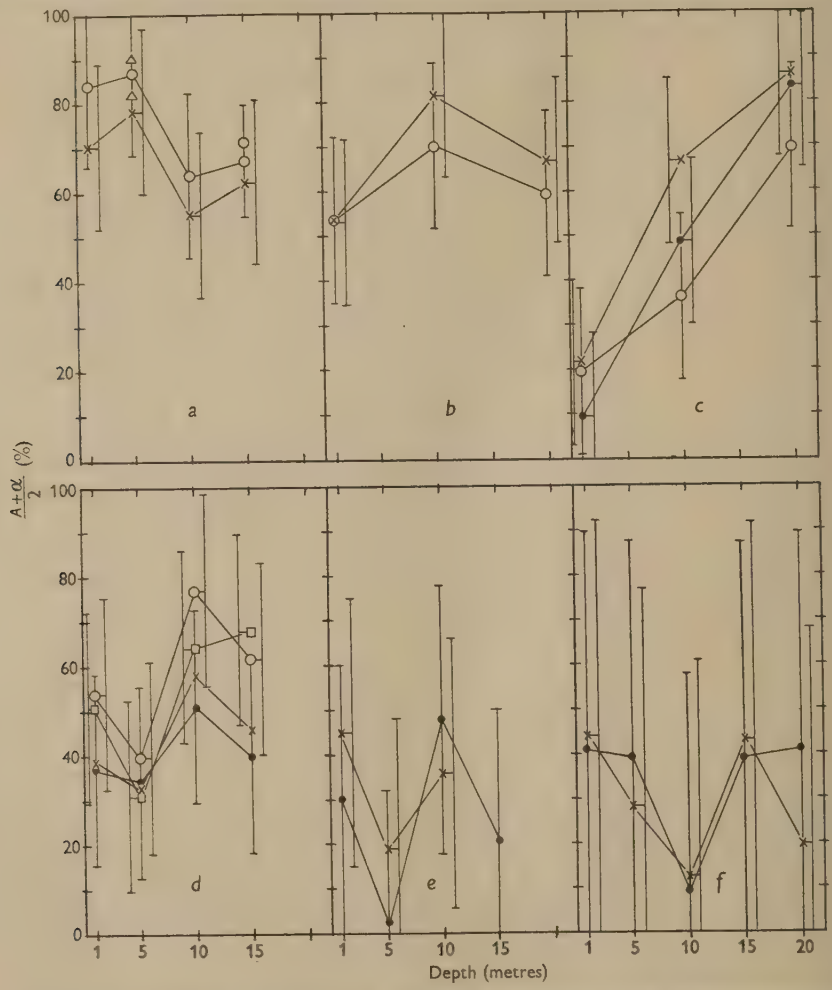

Fig. 3. Results of daylight experiments with the double standard apparatus in Windermere; *a*, *b*, *c*, 1 h duration, 1939; *d*, *e*, *f*, 15 min duration, 1947. *a*, *Diaptomus gracilis* from 15–0 m (experiments 4–8) and from 10 to 0 m (experiment 9). *b*, *D. gracilis* from 30 to 0 m (experiments 1–3). *c*, *Cyclops strenuus* from 30 to 0 m (experiments 1–3). *d*, *e*, *f*, *D. gracilis*, *d*, from 50 to 0 m (experiments 35–38), *e*, from 40 to 30 m (experiments 26–29), *f*, from 50 to 40 m (experiments 30 to 34). ○, stage III. ●, stage IV; ×, stage V; ⊗, male; □, female; △, experiment 9; vertical lines show the values of $\pm 2\sigma$.

In considering the deep origin experiments in detail, it will be recalled that the variance on each observation was overestimated, and that the bias included in the variance was due to the animals tending to remain where they were put. Table 3

shows that the percentage in α is smaller than that in A, particularly in experiments 30–34, the deepest set. This is as if the animals were either merely sinking or reacting slowly. Little weight is attached to the significance of any one observation in experiments 26–34, but greater weight can be attached to the consistency of observations. Downward aggregation takes place at 5 m in experiments 26–29 and is most marked at 10 m in experiments 30–34; in both sets of experiments, downward aggregation was much less apparent at 1 and at 20 m (except *D. gracilis* V at 20 m). The pattern of aggregation in experiments 26–29 may not appear to be very clear. It will be recalled that the light intensity at 15 m was greater than that at 10 m and as it will appear later that light intensity is possibly the mediating factor in these experiments, the observations at 10 and 15 m should perhaps be exchanged in depth. Again, it is worth noting that where the depth of downward aggregation was at 5 m, the depth of plankton origin was 30–40 m and that where the depth of downward aggregation was at 10 m, the depth of plankton origin was 40–50 m.

There are three conclusions: first, it is possible that there is a relation between the depth of aggregation, upward or downward, and the depth of plankton origin. Secondly, in three cases out of four, aggregation, upward or downward, is most marked at a middle depth, and less so at shallower and greater depths. Thirdly, the downward aggregation shown by *Cyclops* in the shallow-origin series was different from that shown by *Diaptomus* in the deep-origin series, in that the number of the latter in A equalled the numbers in α. Yet it is thought that the phenomenon shown by *Diaptomus* is the same as that shown by *Cyclops*, but taking place more slowly.

Aggregation varied in the same manner, but in different directions, upward or downward; during the experiments, both depth and light intensity were varied. During the night series, depth was kept constant and light intensity was varied; hence, if changes in aggregation occur in the night series, as they do in the day series, depth as a cause of aggregation may be eliminated.

(*b*) *Double standard, dusk, night and dawn; tendency to aggregation at different times at one depth*

Four sets of experiments were carried out with depth constant and light intensity variable. In Windermere, *Diaptomus gracilis* and *Cyclops strenuus* were used at 5 m in July 1939, and at 1 m in July 1947. Plankton was taken in the early evening with a 180-mesh net; in 1939 this net was used horizontally between 5 m and the surface, and in 1947 it was used vertically between 50 m and the surface. In the North Sea, in July 1948, *Temora longicornis*, *Calanus finmarchicus* and *Pseudocalanus elongatus* were used in two sets of experiments at 10 m and at 70 m; plankton was taken just before the experiments in each set were started, with a Clarke-Bumpus net hauled vertically from 70 to 50 m.

(i) *Windermere*

Experiments 14–20 (Fig. 4) were made in Windermere (1939) on *Diaptomus gracilis* males and females between 1940 and 0700 h G.M.T. The first experiment was carried out about half an hour before sunset and all animals aggregated downwards. This

state persisted in all experiments until 0100 h. Between 0300 and 0500 h, however, the male *Diaptomus* aggregated neither upwards nor downwards; the female *Diaptomus* showed a similar tendency at the same time, but a downward aggregation nevertheless took place. The lack of aggregation and the tendency towards this state took place at the time of dawn.

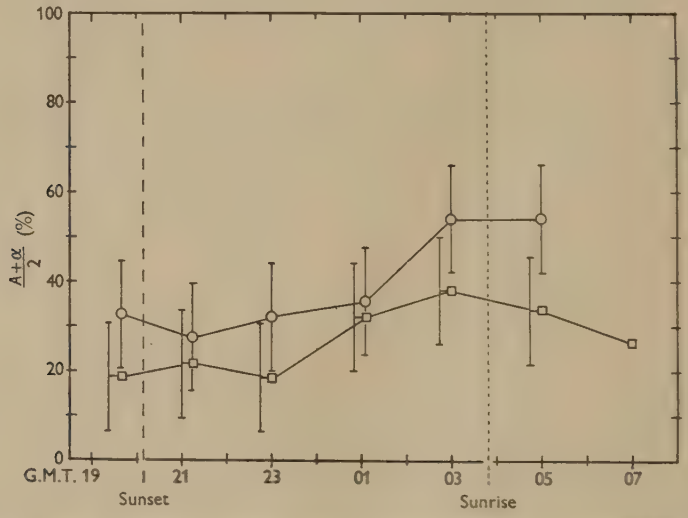

Fig. 4. Dusk to dawn experiments (14–20) in 1939 using the double standard apparatus with *Diaptomus gracilis* from 5 to 0 m. All experiments were made at 5 m except that at 2300 h, which was made at 1 m. ○, male; □, female.

Experiments 54–60 (Fig. 5) were made in Windermere (1947) on *Diaptomus gracilis* IV, V and female and *Cyclops strenuus* IV and V between 1810 and 0620 h G.M.T. The first experiment was carried out 2 h before sunset and both *Cyclops* stages were aggregated at the bottoms of the tubes; *Diaptomus*, however, was not aggregating either upwards or downwards. *Diaptomus* was in the same state at sunset, and *Cyclops* stage V was aggregated at the top of the tubes and *Cyclops* stage IV showed a tendency towards upwards aggregation. In full darkness, *Diaptomus* aggregated downwards; neither *Cyclops* stage showed an aggregation, but later they showed a downward aggregation. In the dawn, *Diaptomus* showed no aggregation and *Cyclops* a downward one.

Common to all movements in these sets is a downward movement in full darkness. Rose (1925) observed that copepods in darkness tended to sink or to move at minimal speeds. An analysis of published observations on vertical migration led me (1951) to postulate that animals which had reached the surface by dusk sank slowly for a small distance during full darkness until, in the dawn, they rose again to the surface; this phenomenon I called midnight sinking. The states of no aggregation and upward aggregation are certainly active, but downward aggregation could be active or passive. In *Diaptomus*, the downward aggregation of full darkness is preceded by activity at dusk and followed by activity at dawn; in this way it is analogous to the midnight sinking found in field observations. From experimental observations light intensity

appears to induce active movement in the animals, hence it is possible that the downward aggregation in daylight is an active movement and that the downward aggregation in full darkness is truly a midnight sinking. Thus the downward aggregation in daylight by *Diaptomus* of deep origin is not considered as a passive sinking, but as a slow movement. It is interesting to note that at the strongest light intensities in the deep water experiments the percentages in A and α are more nearly equal.

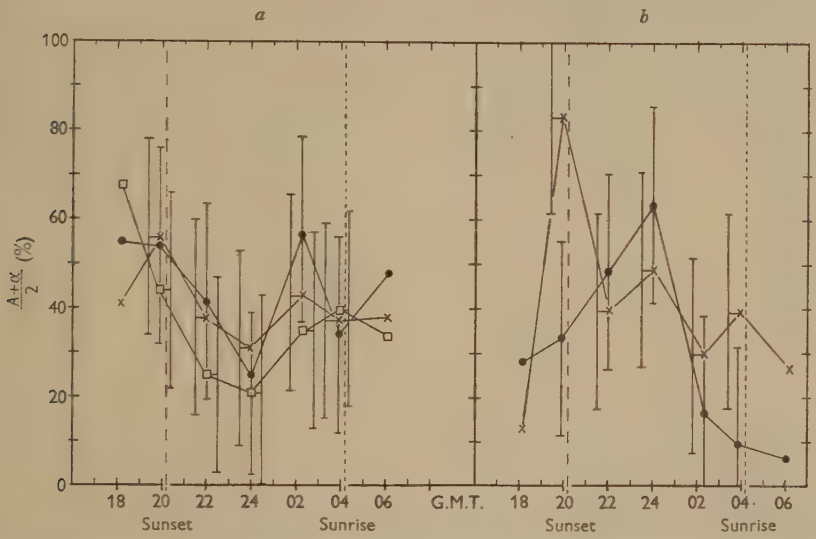

Fig. 5. Dusk to dawn experiments in 1947 with the double standard apparatus at 1 m (experiments 54–60). *a, Diaptomus gracilis; b, Cyclops strenuus.* For symbols see Fig. 3.

If this interpretation is correct, then the active aggregations would take place at dusk and dawn. At dawn, *Diaptomus* makes no aggregation, whereas both stages of *Cyclops* aggregate downwards; if the latter is an active movement, then *Cyclops* is moving down before *Diaptomus*. At dusk *Diaptomus* again makes no aggregation, whereas *Cyclops* IV aggregates downwards and *Cyclops* V aggregates upward. If the downward movement of *Cyclops* IV is active, then *Cyclops* is probably moving up later than *Diaptomus*.

If these aggregations bore any relation to vertical migration, one would expect that the differences between *Diaptomus* and *Cyclops* in aggregation at dusk and dawn were related to differences in day depth, as are differences in times of surfacing (Cushing 1951). Both in 1939 and in 1947 a series of vertical hauls was taken with a closing net in full daylight from 5–0, 10–5, 20–10, 30–20, 40–30, 50–40 and 56–50 m. The distributions are shown in Fig. 6; the scale of numbers is a logarithmic one and a coefficient of variation of 100% has been assumed. In 1939 clearly and in 1947 less clearly, there was a tendency for *Diaptomus* to be found at shallower levels in daytime than *Cyclops*; in 1947, it is possible that *Cyclops* IV lay in a somewhat deeper level than did *Cyclops* V.

Relating this result to those from the double standard apparatus, the shallow

Diaptomus makes no aggregation in the dawn when the deeper *Cyclops* is already moving downwards. At dusk when again *Diaptomus* makes no aggregation, the deeper *Cyclops* is still aggregating downwards. We may describe *Diaptomus* as an afternoon

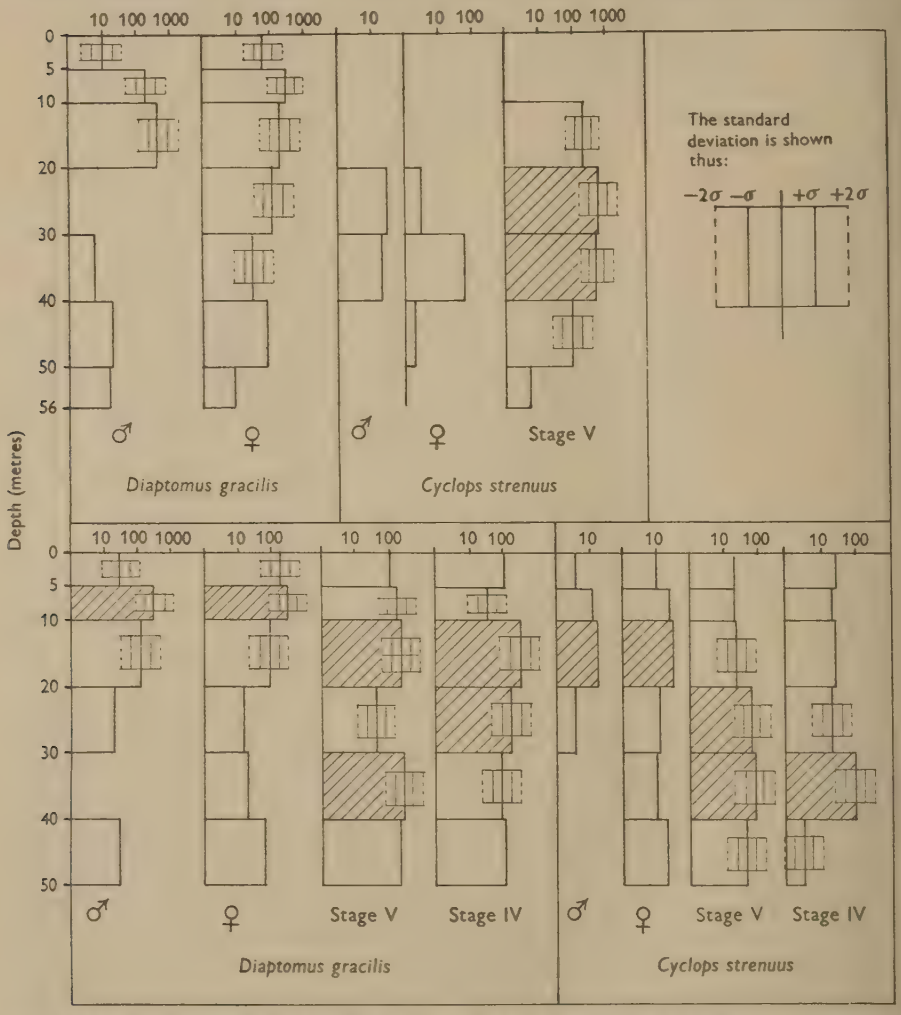

Fig. 6. The vertical distribution of *Diaptomus gracilis* and *Cyclops strenuus* in the daytime (from vertical hauls with a closing net); above, in 1939; below, in 1947. Numbers are represented horizontally on a logarithmic scale. Cross hatching indicates the depths from which the greatest numbers of any one sex or stage were caught.

migrant, living in the daytime in shallow levels, reaching the surface in the late afternoon and sinking away from the surface in full darkness, to return at dawn before descending to its day depth. *Cyclops* V is an evening migrant reaching the surface at sunset and *Cyclops* IV is a night migrant, reaching the surface in full darkness.

In the daylight experiments, *Cyclops* IV and V aggregated downward at 1 m and upwards at 20 m; in the night series, *Cyclops* IV and V aggregated downwards before sunset and upwards after sunset. In the daylight experiments, the difference between the two forms of aggregation could be attributed to variations in depth or light intensity; in the night series, however, carried out at constant depth, the same difference can only be attributed to light intensity. It is significant that as light intensity decreased *Cyclops* V aggregated downwards and then upwards; *Cyclops* V aggregated downwards in the daylight at 1 m and upwards at 20 m, where the light intensity was considerably reduced, compared with that at the surface. If it is accepted that light intensity is the mediating factor in these experiments, then it is reasonable to write that the animals living deeply in the daytime and migrating late are responding to lower levels of light intensity than those that live shallow and migrate early.

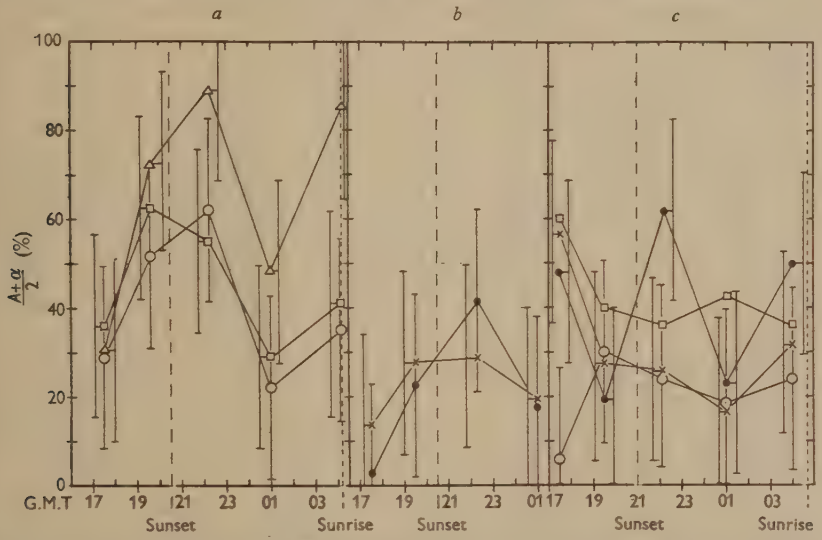

Fig. 7. Dusk to dawn experiments (67–71) with the double standard apparatus at 10 m in the North Sea in 1948. *a*, *Temora longicornis*: ○, males; □, females; △, juveniles. *b*, *Calanus finmarchicus*: ●, stage IV; ×, stage V. *c*, *Pseudocalanus elongatus*: ○, males; □, females; ●, stage IV; ×, stage V, vertical lines— $\pm 2\sigma$.

(ii) *North Sea*

Experiments 67–71 (Fig. 7) were made at 10 m between 1730 and 0425 h G.M.T. It is possible that the juveniles of *Temora longicornis* show within the tubes the whole pattern of vertical migration. In the evening before sunset they aggregated downwards, and by 2230 h an upward aggregation had taken place; later, during full darkness, the upward aggregation was reduced to none; in the light of dawn, however, the animals aggregated upwards. It is possible that these movements reflect the components of vertical migration in the sea—ascent from the day depth to the surface, midnight sinking and dawn rise; these particular observations show no descent to the day depth in the morning. It is interesting to note that *T. longicornis* male and female made aggregations that followed the same trends as those of the juveniles, but of

different character. This implies that there is only a difference of degree between, for example, the lack of aggregation on the part of the adults, and the upward aggregation by the juveniles in the dawn and in the dusk.

The same experiments show that *Pseudocalanus* makes no aggregation in the evening and a downward aggregation in full darkness; there is thus a resemblance between the experiments on *Pseudocalanus* and those on *Diaptomus*. The observations on *Calanus* show a downward aggregation in the evening, no aggregation at sunset, followed by another downward aggregation in full darkness; there is a resemblance between these observations and those on *Cyclops* IV. Following the terminology used in the previous section, *Pseudocalanus* is like *Diaptomus*, an afternoon migrant, *Temora* is like *Cyclops* V, an evening migrant and lastly *Calanus* resembles *Cyclops* IV, a night migrant.

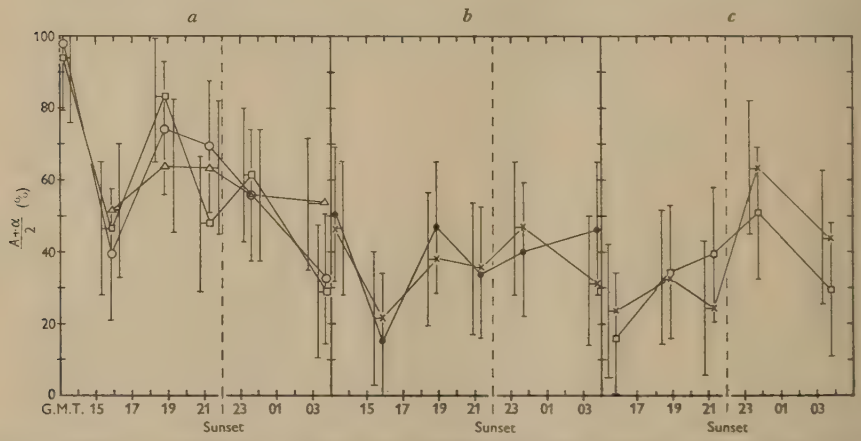

Fig. 8. Midday to full darkness experiments (61–66) with the double standard apparatus at 70 m in the North Sea in 1948. *a, Temora longicornis; b, Calanus finmarchicus; c, Pseudocalanus elongatus.* For symbols see Fig. 7.

Experiments 60–66 (Fig. 8) were made at 70 m between 1300 and 0400 h G.M.T. This set of experiments was remarkable for a strong difference in light intensity (which was, in 1948, not measurable at 70 m.); by 1600 h, the sun had come out from an overcast sky and the state of sea had dropped from 2 to 0. The increase in light intensity at 70 m had the following effects: (*a*) the very sharp upward aggregation by adult *Temora* is reduced to none, (*b*) the lack of aggregation by *Calanus* becomes a downward one, (*c*) the downward aggregation of *Pseudocalanus* is reduced to none. If these animals were responding to the change in light intensity, it appears that the aggregation of *Temora* is related directly to light intensity, the aggregation of *Calanus* is related inversely to light intensity and *Pseudocalanus* possibly did not respond at all. Similarly, in full darkness it is likely that no aggregations took place at 70 m.

(iii) *Conclusion*

From the night series of experiments (Experiments 14–20, 54–60, 67–71, 61–66), we may conclude that migrations, related to time of day, and hence probably to light intensity, may be shown to take place in the double standard apparatus. Furthermore,

the deeper-living animal of a pair—*Cyclops* deeper than *Diaptomus* in Windermere and *Temora* than *Pseudocalanus* in the North Sea (Savage 1926, 1931)—moves upward later, as darkness approaches. From the experiments it appears that *Calanus* responds to a lower level of light intensity, migrating later, than *Temora*; however, the difference between the levels of abundance is not greater than the error that should be attached to any one observation.

(*c*) *Long-tube experiments—Windermere*

It will be recalled that the long tube consists of seven sections, A, B, C, D, E, F and G, the last being the bottom one. Plankton animals may be put in any section and, by means of the apparatus, their movement away from it estimated. It is possible to

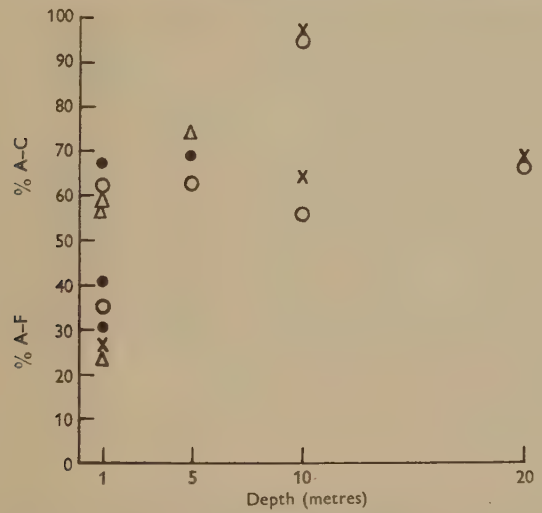

Fig. 9. Results of long-tube experiments with *Diaptomus gracilis* treated as if the long tube were one of a pair of double standard tubes. ×, stage IV; ○, stage V; ●, females; △, males.

compare results from the long tube with those from the double standard apparatus. When plankton is put into section G or section D of the long tube, the percentage of animals that have climbed into sections A–F or sections A–C is comparable with the percentage of animals that have climbed into section α in the double standard apparatus. Fig. 9 shows results from long-tube experiments arranged in this manner, using *Diaptomus* IV, V, male and female, taken in full daylight in vertical hauls from 40 to 0 m; thus the experiments are roughly comparable with experiments 1–3, for which the plankton was taken from 30 to 0 m. It will be seen from Fig. 9 that upward aggregation is greatest at 10 m and is less at 1 and 20 m; this result is quite comparable with experiments 1–3 and if comparison is extended, it will be noted that there is a tendency for downward aggregation at 1 m and a tendency for upward aggregation at 20 m, which is perhaps related to the somewhat greater depth of origin of the plankton used in the long-tube experiments.

Experiments 39–46 were carried out to find the effect on aggregation of different durations: durations were 30, 1, 2, 3, 4, 5, 10 and 20 min respectively. This was done in order to find out whether reasonable results could be obtained with the double standard apparatus in 15 min (1947 series) rather than in an hour (1939 series). Each experiment was carried out with the top of section A at the surface and the plankton animals were always placed in section G.

Some diaptomids and a *Daphnia* were able to climb the full length of the long tube in 1 min, i.e. 3·5 m min. At this speed, they could climb through the whole water column in Windermere (70 m) in about a quarter of an hour. It has been shown that diaptomids spend all the time from noon to dusk in climbing from 35 m to the surface (Ullyott 1939), so the real speed of migration (about 4 cm min) must be well within their powers: as the animals can move ninety times as fast as this, it seems possible that the zone of aggregation is a zone of slow movement.

Measurements of light intensity were made at the surface during each experiment. The underwater cell was not in use during this set of experiments and so results are expressed only as 'galvanometer units' from the deck cell.

Experiments 39 and 40 lasted 30 and 1 min respectively; the light intensity, as measured by the deck cell, was the same in each experiment. The percentages in section G were 46 and 76% respectively. Let it be assumed that the difference of 30% is only an effect of 29 min continuous movement under the same conditions of light intensity; similarly, it may be assumed that the effect of 10 min continuous movement would make a difference of 10/29 of 30%, i.e. 9·8%. For all experiments in the duration set, similar adjustments for continuous movement at one light intensity were made; it is then assumed that the remaining differences are related to differences in light intensity. The steps are set out in Table 2.

Table 2. *Adjustments for duration in the duration series of experiments*

Duration in min ...	1	2	3	4	5	10	20	30
Percentage in G	76·3	43·7	60·8	45·5	83·6	34·3	58·3	46·8
Difference in duration from Expt. 39 (min.)	29	28	27	26	24	20	10	0
Adjustment	28·6	27·6	26·6	25·6	24·6	19·8	9·8	0
Adjusted percentage in G	47·7	16·1	34·2	19·9	59·0	14·5	48·5	46·8
Light intensity in galvanometer units	4·6	8·2	8·5	11·9	5·0		6·6	4·6

Fig. 10 shows the adjusted percentages plotted against the light intensity: it will be seen that there is a negative regression of adjusted aggregation on light intensity. This means that the stronger the light intensity, the fewer animals remain in section G: larger aggregations occur in section G when the light intensity at the surface is lower. Thus the degree of downward aggregation is inversely proportional to the light intensity. It will be noticed that the observations at 1 and 2 min about the regression are not significantly different from those at longer durations: this means that reasonable results can be obtained from 15 min experiments, although they are only qualitatively comparable with those carried out for 1 h. No more than qualitative comparisons have been made between sets of experiments each of which lasted an hour and sets each of which lasted 15 min.

If the degree of aggregation is related to light intensity, a possibility supported by the results of the double standard experiments, then differences assumed in Table 2 should also be part of the same effect. If animals were moving randomly in direction in the long tube, as they appear to do, then it might be reasonable to treat the results as if animals had diffused from the originating sections. At different light intensities their mean speeds of diffusion would be different. Fig. 11 shows the long-tube results for the duration series of experiments arranged by plotting the percentages in sections transformed by logs against the distance (squared) through which the animals have moved to reach the section in which they were found at the end of the experiment. It will be noticed that a linear fit to most of the regressions would be adequate.

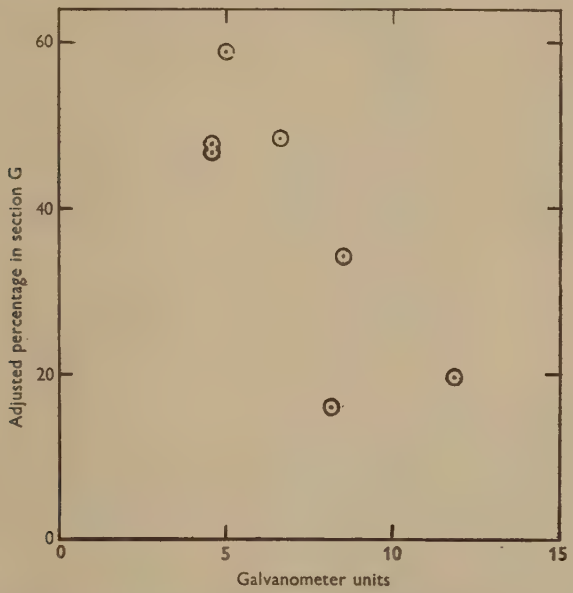

Fig. 10. Relation between light intensity and the adjusted percentage in section G, from the duration series of experiments, for *Diaptomus gracilis*, stage V.

A number of long-tube experiments were carried out at different depths and under different conditions. The results are given in Tables 5 and 6, Appendix. No analysis of these results has been attempted because the effect of light intensity on aggregation has not been clearly enough separated from the effect of duration. This might not matter very much if all experiments were of the character shown in Fig. 11, where the 'rates of diffusion' did not vary very much; in a number of experiments, however, the distributions are totally different and a laboratory programme would probably be necessary to elucidate them.

However, there is one result that can be used and it is concerned with the effect of temperature. Experiment 51 was a long-tube experiment, with the plankton put in section A at 12 m. The tube was set across the thermocline, the temperature measurements being shown in Fig. 12; the discontinuity is not very sharp, but there was

a considerable temperature difference within the tube. Fig. 13 shows a comparison between experiment 49 at the surface and experiment 51 at 10 m for *D. gracilis* IV and V. The temperature difference has had little effect on the distribution of descending animals; the marked difference in light intensity also appears to have no effect. If these results were treated as double standard results, one would say that no aggregation was taking place.

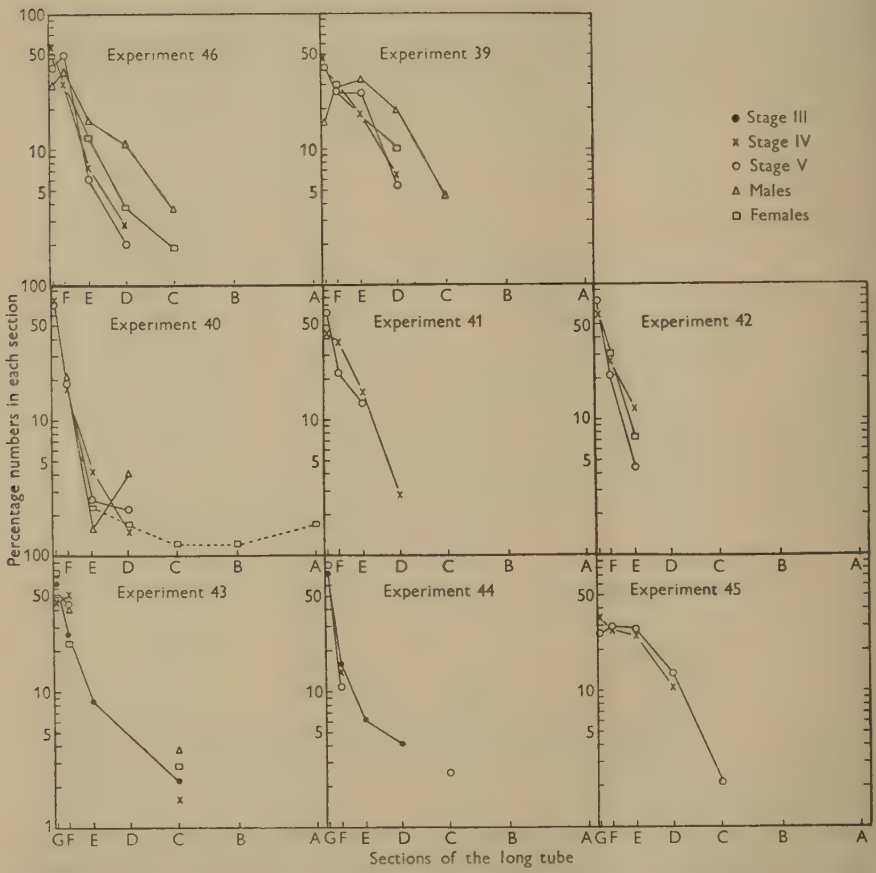

Fig. 11. Long-tube experiments with *Diaptomus gracilis* on duration, in which log n (where n = percentage numbers in each section) is plotted against d^2 (where d is the distance from the originating section). All experiments were carried out with section A at the surface.

DISCUSSION

The daylight experiments with the double standard apparatus showed that between 1 and 20 m, the shallow *Diaptomus* plankton aggregated upwards, whereas the deep *Diaptomus* plankton aggregated downwards. The two forms of behaviour, upward and downward aggregation, resembled each other in that both appeared most markedly

at 10 m and less markedly at the extreme depths of 1 and 20 m. For *Cyclops strenuus*, however, it was shown that the upward aggregation succeeded the downward aggregation as experiments were made at successively greater depths, down to 20 m.

In the dusk to dawn series of experiments, the two forms of aggregation appeared at the same depth at different times, during dusk and dawn. As changes in light intensity are common to both the night and the daylight series and change in depth occurs only in the latter, it is reasonable to conclude that the change in aggregation observed in both sets of experiments is related to change in light intensity. Further, it was noticed at dusk that upward aggregation succeeded downward aggregation as light intensity decreased—*C. strenuus* IV and V, Fig. 5 and *Temora longicornis*, Fig. 7

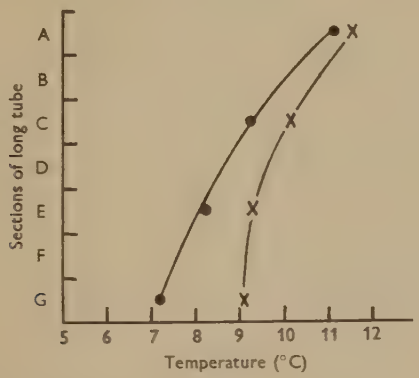

Fig. 12. Temperature distributions for experiments 51 and 52.

(as indeed happened to *Cyclops strenuus* in daylight experiments as light intensity decreased with increasing depth). There is some evidence from the duration experiments in the long tube that the density of aggregation was related to light intensity, in this case inversely, i.e. as light intensity increases, downward aggregation becomes less sharply marked. There are thus three independent points of evidence suggesting that the changes in aggregation described in these experiments were mediated by light intensity.

These results may be related to published data on the correlation between migration and light intensity. The continuous change of day depth of migrants has been correlated with a continuous change of light intensity within one or more periods of 24 h (Russell 1934, Clarke 1933, Ullyott 1939). Variations in the day depths of migrants with different conditions of light penetration have been correlated by Russell (1926*c*) and Russell & Colman (1934). Numbers of plankton animals at the surface at night are greater at the periods of full moon (Francé 1894, Steuer 1902, Moore 1949); again, Lozéron (1902) showed that four zooplankton species were nearer the surface on nights of bright moonlight than on nights when the moon was darkened by cloud. Lastly Ruttner (1914) found that three zooplankton species were higher in the water before snow had been swept off the ice of a frozen lake; when he cut windows in the ice, the plankton animals took up a lower level in the lake.

If plankton animals were responding to light intensity, it would be reasonable to expect their day depths to be related both to their times of surfacing and to the character of their migrations. Such a relation was postulated from published results (Cushing 1951); from the experiments described here, it is shown that the shallow *Diaptomus* and *Pseudocalanus* are afternoon migrants, that the somewhat deeper

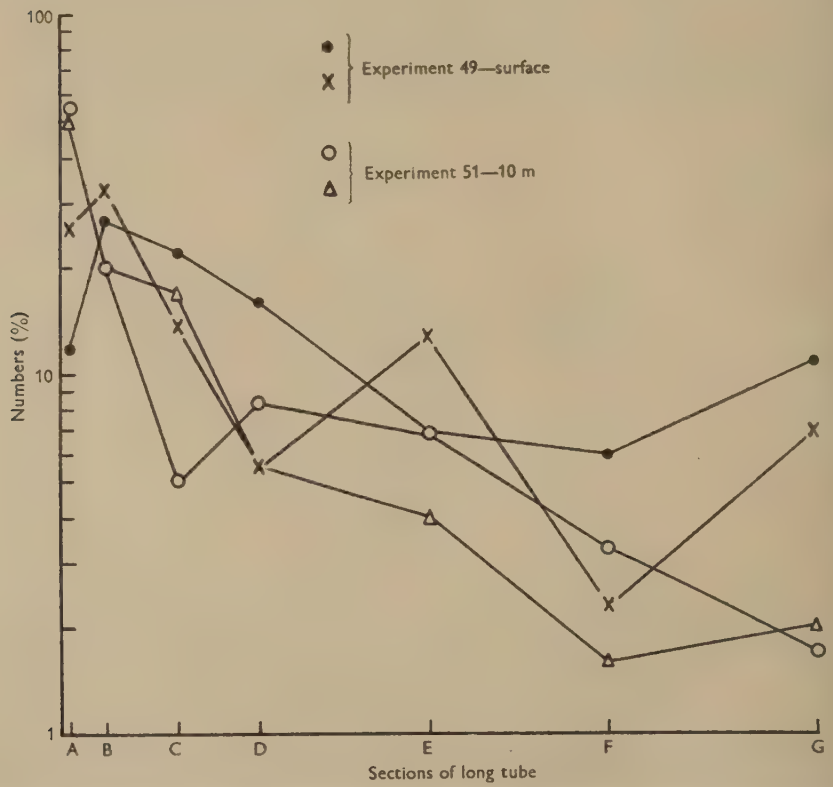

Fig. 13. Distributions of experiments at the surface and across a thermocline plotted as for the duration experiments, for *Diaptomus gracilis* stages IV and V; the animals were descending from section A.

Cyclops V and *Temora* are evening migrants and possibly that the yet deeper *Cyclops* IV and *Calanus* are night migrants. It was thought that the aggregations found in the double standard apparatus changed in accordance with changes that a vertical migration would bring about; this was most strongly shown by *Temora longicornis* juveniles, the aggregations of which followed the migration movements of ascent, midnight sinking and dawn rise. Now, if the aggregations described both in the day and night series of experiments were mediated by light intensity, it would be reasonable to extend the effect to the relation between day depth (or depth of plankton origin) and surfacing time, to the character of migration and even to the phenomenon of vertical migration itself. This is the basis of the hypothesis that plankton animals are found in daytime

in an optimum band of light intensity, hence restricted to a particular depth-range. The development of this hypothesis may be found in the works of Michael (1911), Rose (1924, 1925, 1929) and Russell (1926–34); the clearest statement of the hypothesis is that of Russell: 'Intensities of light may inhibit or stimulate movement; in certain forms, high intensity produces negative phototropism and low intensity produces positive phototropism; at an intermediate intensity the animal is neutral.'

If the animals are responding to light intensity, aggregation as observed in the tubes can be generated in two ways: (*a*) *phototactically*, individuals moving vertically towards the light at constant speed would form an upward aggregation at the top of the tube; (*b*) *photokinetically*, individuals moving randomly in direction, moving more rapidly in dim light than in strong, would also form an upward aggregation. A most important difference is that when 'phototactic' animals responded directly to light intensity, 'photokinetic' animals would have been responding inversely to light intensity. A state of no aggregation in daylight is described phototactically as being manifested by a mixed population of positive and negative animals and photokinetically as a case in which there is no change of speed for the change of light intensity within the vertical distance of the tube.

In migration, phototactic animals would move vertically in depth between two light intensity levels and the sign of the taxis would change from positive to negative at the high intensity level and from negative to positive at the low intensity level. The zone between the two levels of light intensity would be the optimum band, approached by negative animals from above and by positive animals from below. Photokinetic animals would move randomly in direction, but more slowly in the zone of optimum light intensity at which they aggregate from above and below; above the optimum level, the animals' speeds would be directly related to light intensity and below it, speeds would be inversely related to light intensity. It must be pointed out that in the experiments described in this paper, the very act of enclosure of the animals in tubes may impose an apparently random movement on the animals.

One objection to photokinesis is that migrating animals are said not to move randomly in direction. Bainbridge (1952, 1953) has observed *Calanus* within a few feet of the surface in a calm sea; he reports that within 1 ft of the surface, movement is randomly directed and erratic, but that below this zone *Calanus* moves straight up or straight down. It appears from Bainbridge's papers that *Calanus* is the only planktonic animal that he observed to behave in this way; this confirms observations made by the late Lt-Cdr Hodges, R.N.V.(S)R., an experienced frogman, that the planktonic animals (*Diaptomus* and *Cyclops*) down to 10 m in Windermere move in all directions and do not make steady up and down movements. Perhaps it is possible that deeply living *Calanus* (from 70 to 80 m in the Cumbrae Deeps) on reaching the surface region by random excursion, behaved phototactically in calm weather (cf. Cushing 1951). When I have watched animals in the double standard apparatus or in the long tube, it has appeared to me that the animals were moving randomly in direction; this might well be merely the effect of enclosure, but it seems that the underwater observations in general make the condition realistic. Professor Hardy

has told me that he finds it difficult to believe that euphausiids climb from 250 m to the surface in about 2 h, merely by random movement (Hardy & Gunther 1935). It is, however, possible that *Euphausia frigida* (male, female and immature) and *E. triacantha* avoid the net in daytime.

Some of the details of the daylight series of experiments made in Windermere can be explained best by a photokinetic hypothesis. It will be recalled that animals aggregated upwards or downwards most at middle depth and least at the shallow and the extreme depths of experiment. If the animals were really moving randomly in direction, an aggregation could be caused by a speed difference within the tube, i.e. they would crowd at the end at which they were moving most slowly. This speed difference within the tubes would be small at the extreme speeds, both slow and fast, but would be greatest at middle speeds. Aggregations occurred at the middle depths but not at the shallow and the extreme depths; it is possible that the animals were moving at a medium speed at the middle depths, but at the shallow and extreme depths were moving either very rapidly or very slowly. It will be recalled that the shallow *Diaptomus* plankton aggregated upwards in the double standard apparatus most markedly at a middle depth. Perhaps they do not aggregate at the greater depth because they are moving so slowly that there is no difference in speed within the length of the tubes; the same effect could appear at shallow depth as a consequence of moving at maximum speed. The similar pattern in downward aggregation shown by the deep *Diaptomus* plankton is perhaps due to a similar effect, i.e. the lack of aggregation is caused by slow movement at the surface and rapid movement at 20 m. We have seen that one plankton species can exhibit both upward and downward aggregation (*Cyclops strenuus*, experiments 1–3; experiments 54–60; *Temora longicornis*, experiments 66–71). It has been shown that the extent of downward aggregation is inversely related to light intensity; perhaps one might assume that the extent of upward aggregation is directly related to light intensity. If this is so, it is suggested that the optimum zone is one of slow movement, and that above it animals respond directly to light intensity (aggregating downwards in the tubes), and that below it animals respond inversely to light intensity (aggregating upwards in the tubes). Hence the optimum zone would be characterized by lack of aggregation and sharp aggregations would only appear in regions fairly close to the optimum zone in depth, where animals moved at medium speeds; it also follows that lack of aggregation would also appear in regions remote from the optimum zone, where animals moved at maximum speeds.

In an analogous type of apparatus, results have been interpreted in the following way (Thorpe, Crombie, Hill & Darrah 1947):

Let the mean velocity of animals in sections A or α be w.

Let the mean velocity of animals in sections B or β be v.

Let the mean velocity change from w to v as animals move from A to B or from α to β.

At an equilibrium state, let there be a animals in sections A or α and b animals in sections B or β.

Then the number of animals moving from A or α to B or β will be aw and the number of animals moving in the other direction will be bv.

At equilibrium, $$aw = bv,$$

therefore $$1 + \frac{w}{v} = \frac{a+b}{a}.$$

From this equation, the ratio of speed in the upper half of the apparatus to that in the lower half can be related to the percentage numbers in the sections. It was estimated above that the mean speed of ascent of diaptomids in Windermere was 4 cm min. Assuming that this is the mean upward speed in the optimum zone, the maximum mean speed as shown in the double standard results is 40 cm min. This is not unreasonable as diaptomids were shown to have a speed in a straight line of at least 350 cm/min.

If plankton animals migrate vertically by photokinesis, the majority remain in the optimum zone moving quite slowly up to the phytoplankton zone by dusk. The whole system allows the animals to obtain maximum grazing with the use of the least energy at the least risk of predation. For phototactic animals such a system would be a little more complicated and no energy would be saved.

Fig. 14 gives a diagrammatic representation of the photokinetic hypothesis in terms of the mean speeds of the animals and in terms of results from the double standard experiments.

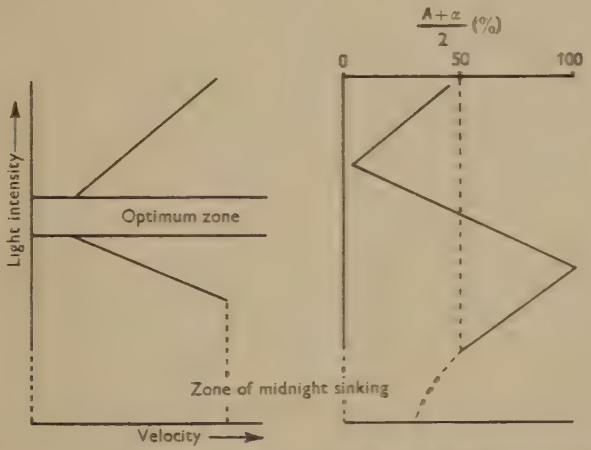

Fig. 14. The position of an optimum band in the sea in relation to the distribution of $A - x^2$ in the experimental series and to a possible interpretation of the results.

It will be noticed that a zone of midnight sinking is placed in deep water; although this concept finds its application in the dusk–dawn experiments, there is a depth in the sea at which either there is no light at all or so little that the animals do not respond to it.

Harris (1953) has formulated a hypothesis to account for the migrations of *Daphnia magna* in tubes. At low light intensity the animals show positive photo-orthokinesis with geotactic orientation, and at a higher light intensity a dorsal light reaction supervenes, which serves to retain the animal within the band of optimum light

intensity. I have observed *D. hyalina* swimming near the surface in Windermere in the upright manner described by Harris for *D. magna*; *Diaptomus* and *Cyclops*, however, swam oriented in all directions. Nevertheless, this hypothesis could be used to account for many experiments described in this paper; 'photokinesis' in this paper expresses the effect of light intensity on a variety of movements without specifying the relation to any one of them.

ACKNOWLEDGEMENTS

Professor A. C. Hardy, F.R.S., introduced me to this problem and encouraged me in its development; for his help and his criticism, I am fully grateful. I must also thank Mr G. M. Spooner for much critical assistance and Mr J. A. Gulland for examining my statistics.

SUMMARY

1. Using the 'double standard' apparatus at various depths (down to 20 m) in daylight in Windermere, it was found that *Diaptomus gracilis* of shallow origin tended to be found in the top of the tubes, whereas *Diaptomus* of deep origin tended to be at the bottom. For *Cyclops strenuus* of 'shallow' origin, which was probably from a deeper layer than the *Diaptomus*, as experiments were carried out at progressively deeper layers, downward aggregation was succeeded by upward aggregation.

2. In Windermere, several species, when tested at the same depth at different times near and during darkness, showed a tendency to reverse their initial reaction as light increased or decreased. For example, *Cyclops strenuus* in the evening was down, and as the light decreased it rose. For several species, the behaviour at constant depth, with light varying was similar, and in certain species identical, to that found at varying depths during daylight. This provided an indication that light, rather than depth, was the mediating factor in migration.

3. There was a rough relation between the depth at which the forms were found in daylight and the character of the migration that they showed in series of experiments at constant depth at dusk, night and dawn. This was true both in Windermere and in the North Sea. The forms in question were: *Diaptomus gracilis*, *Cyclops strenuus* stage IV, *C. strenuus* stage V, *Pseudocalanus elongatus* and *Temora longicornis*. The patterns of migration in these were classed as 'afternoon', 'evening', or 'night'.

4. In experiments in the 'Long tube' in Windermere, a few diaptomids and *Daphnia longispina* climbed at a speed of 3·5 m/min. Placing the long tube across a thermocline had no effect on the distribution of descending animals.

5. The experimental aggregations are discussed in relation to the observed vertical migration in the sea. It is pointed out that the movements of animals making such migrations could be phototactic or photokinetic. Some evidence is put forward that, within the tubes at any rate, plankton animals were behaving photokinetically.

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APPENDIX

Table 3. *Results of double standard experiments in Windermere, 1939 and 1947*

The percentage of animals in A and α, the mean percentage in A and α, and the number of animals contributing to the percentage are given for each species.

Expt. no.		Time (G.M.T.)	Sea	Weather	Temp. (° C)	Depth (m)	Species	Stage	A	α	$\frac{A+\alpha}{2}$	n
	1939											
2	9 June	1551–1651	1	Sun, N. breeze	19·4	1	*Diaptomus gracilis*	III	58	49	53·5	639
								V	56	50	53·0	434
							Cyclops strenuus	III	25	14	19·5	362
								IV	8	11	9·5	601
								V	17	26	21·5	535
3	10 June	1110–1210	0–¼	Overcast, drizzle	11·1	10	*Diaptomus gracilis*	III	73	67	70	420
								V	86	77	81·5	472
							Cyclops strenuus	III	53	19	36	342
								IV	62	35	48·5	380
								V	79	54	66·5	419
1	9 June	1356–1456	0–¼	Sun, S. breeze	8·5	20	*Diaptomus gracilis*	III	50	68	59	678
								V	61	72	66·5	522
							Cyclops strenuus	III	83	56	69·5	943
								IV	90	77	83·5	1339
								V	83	89	86	887
8	16 June	1448–1548	¾	Sun, Fresh S.W. breeze	16	1	*Diaptomus gracilis*	III	73	96	84·5	32
								V	70	71	70·5	230
9	12 June	—	—	—	—	5	*D. gracilis*	III	73	67	70	326
								V	86	73	79	676
									67	71	69	320
							Cyclops strenuus	III	53	19	36	33
								V	79	54	66·5	121
7	16 June	1310–1410	0–¾	Cloudy, occasional sun	16·3	5	*Diaptomus gracilis*	III	87	87	87	74
								V	78	79	78·5	280
6	16 June	1121–1221	0–¾	Cloudy, W. breeze	10·6	10	*D. gracilis*	III	74	54	64	148
								V	79	31	55	519
5	13 June	1312–1412	0	Cloudy, N.N.W. breeze	9·1	15	*D. gracilis*	III	73	70	71·5	231
								V	59	66	62·5	338
4	12 June	1440–1540	½	Cloudy	9·0	15	*D. gracilis*	III	48	76	62	260
								V	60	65	62·5	738
16	4 July	2300–2400	0	Cloud	—	1	*D. gracilis*	♂	24	40	32	424
								♀	16	21	18·5	615
14	4 July	1940–2040	0	Cloud and rain	—	5	*D. gracilis*	♂	28	37	32·5	1107
								♀	12	25	18·5	1528

15	4 July	2115–2215	0	Cloud	—	5	*D. gracilis*	♂	22	33	27·5	428
								♀	18	25	21·5	812
17	5 July	0106–0206	0	Cloud and moon	—	5	*D. gracilis*	♂	38	33	35·5	1437
								♀	33	31	32	2607
18	5 July	0300–0400	¼	Pale sky	—	5	*D. gracilis*	♂	46	62	54	326
								♀	31	45	38	588
19	5 July	0500–0600	¼	Cloud	—	5	*D. gracilis*	♂	46*	62*	54	47
								♀	31	36	33·5	127
20	5 July 1947	0700–0800	0	Cloud, storm approaching	—	5	*D. gracilis*	♀	16	37	26·5	63
21	21 July	0858–0912	1	Rain	—	1	*Daphnia hyalina*	Large	64·4	17	40·7	329
22	21 July	1030–1045	1–2	Heavy rain	—	5	*D. hyalina*	Large	53·6	46·4	50	819
23	24 July	0830–0845	¼	Dull	—	10	*D. hyalina*	Large	4	29·9	16·95	189
24	24 July	0950–1005	¼	Dull	—	15	*D. hyalina*	Large	68·2	40·5	54·35	179
25	24 July	1240–1310	¼	Dull	—	20	*D. hyalina*	Large	58·5	51·8	55·15	277
26	27 July	0945–1000	0	Dull	—	1	*Diaptomus gracilis*	IV	22·5	37	29·8	332
								V	40	50	45	257
27	28 July	0905–0920	0	Dull	—	5	*D. gracilis*	IV	0	4·4	2·2	333
								V	27·3	8·2	17·8	115
28	28 July	1020–1035	0	Dull	—	10	*D. gracilis*	IV	78·8	16	47·4	262
								V	45	26	35·5	82
29	28 July	1320–1355	0	Dull	—	15	*D. gracilis*	IV	38	2·3	20·2	71
30	30 July	0830–0845	0	Sun and cloud	—	1	*D. gracilis*	IV	43	38·7	40·9	518
								V	58·4	28·5	43·5	377
31	30 July	0952–1007	0	Sun and cloud	—	5	*D. gracilis*	IV	74	4·1	39·1	168
								V	47·3	8·2	27·8	154
32	30 July	1400–1415	0	Sun	—	10	*D. gracilis*	IV	13	5·2	9·1	428
								V	18·2	6	12·1	148
33	31 July	0845–0900	0	Sun and cloud	—	15	*D. gracilis*	IV	74	3	38·5	818
								V	81·1	5	43·1	538
34	31 July	0954–1009	0	Cloud	—	20	*D. gracilis*	IV	75	6	40·5	264
								V	29·2	9	19·1	148
35	31 July	1253–1308	0	Sun	—	1	*D. gracilis*	IV	47·7	26·1	36·9	1647
								V	40·4	36·6	38·5	414
								♂	57·3	51	54·2	169
								♀	35·3	66·8	51·1	159
36	31 July	1355–1410	0	Sun	—	5	*D. gracilis*	IV	27·5	40·7	34·1	994
								V	27·3	39·5	33·4	400
								♂	44	34·7	39·4	122
								♀	39·1	23·7	31·4	145

Table 3 (*cont.*)

Expt. no.		Time (G.M.T.)	Sea	Weather	Temp. (° C)	Depth (m)	Species	Stage	A	α	$\frac{A+\alpha}{2}$	n
37	1 Aug.	0856–0911	0	Sun	—	10	*D. gracilis*	IV	61·4	40·9	51·2	1601
								V	59	57·5	58·3	417
								♂	87·1	66·6	76·9	153
								♀	75	53·7	64·4	158
38	1 Aug.	0955–1010	0	Sun	—	15	*D. gracilis*	IV	55·1	23·6	39·4	357
								V	51	40	45·5	109
								♂	75	48	61·5	51
								♀	90·3	45·4	67·9	64
54	3 Aug.	1810–1823	0	Sunny	—	1	*D. gracilis*	IV	55	—	55	554
								V	41	—	41	239
								♀	68*	—	68	28
							Cyclops strenuus	IV	28	—	28	50
								V	13	—	13	129
55	3 Aug.	1953–2008	0	Clear	—	1	*Diaptomus gracilis*	IV	75	33	54	1176
								V	66	46	56	1023
								♀	62	26	44	171
							Cyclops strenuus	IV	33	33	33	119
								V	83	83	83	276
56	3 Aug.	2200–2215	0	Moonrise at 2140 h	—	1	*Diaptomus gracilis*	IV	30	53	41·5	1432
								V	25	51	38	458
								♀	17	33	25	129
							Cyclops strenuus	IV	31	65	48	139
								V	36	42	39	154
57	4 Aug.	0001–0016	0	Moon behind thick cloud	—	1	*Diaptomus gracilis*	IV	26	23	24·5	279
								V	30	32	31	239
								♀	32	10	21	132
							Cyclops strenuus	IV	86	40	63	73
								V	69	28	48·5	116
58	4 Aug.	0216–0231	0	Moon below hills	—	1	*Diaptomus gracilis*	IV	52	61	56·5	1663
								V	38	49	43·5	330
								♀	32	38	35	165
							Cyclops strenuus	IV	—	16	16	154
								V	—	29	29	112
59	4 Aug.	0353–0408	0	Dawn at 0355 h	—	1	*Diaptomus gracilis*	IV	37	31	34	1376
								V	32	42	37	191
								♀	35	45	40	120
							Cyclops strenuus	IV	9	9	9	242
								V	48	30	39	89
60	4 Aug.	0605–0620	0	Sun behind high cloud	—	1	*Diaptomus gracilis*	IV	—	48	48	614
								V	—	38	38	180
								♀	—	34	34	92
							Cyclops strenuus	IV	—	6	6	91
								V	—	26	26	58

Table 4. *Results of double standard experiments in the North Sea in July 1948*

Temora longicornis

Expt. no.	Time (G.M.T.)	Sea	Weather	Depth (m)	Males A	Males α	Males A+α/2	Males n	Females A	Females α	Females A+α/2	Females n	Juveniles A	Juveniles α	Juveniles A+α/2	Juveniles n
61	1315–1330	2	Clouds broken	70	96	100	98	64	93	96	94·5	71	—	—	—	—
62	1550–1605	0	Dull	70	35*	44*	39·5	106	49	44	46·5	136	56	47	51·5	98
63	1850–1905	0	Dull	70	80	69	74·5	185	90	77	83·5	152	42	86	64	107
64	2120–2135	0	Dull	70	81	58	69·5	144	49	47	48	95	60	67	63·5	175
65	2340–2355	0	Dull	70	56	56	56	188	50	73	61·5	151	49	63	56	200
66	0345–0400	0	Dull	70	28*	38*	33	103	30	28	29	108	34	73	53·5	57
67	1730–1745	0	Cloudless	10	19	39	29	329	32	40	36	201	5	56	30·5	173
68	1935–1950	0	Some clouds	10	52	51	51·5	134	59	66	62·5	78	53	92	72·5	138
69	2215–2230	0	Stars and cloud	10	56	68	62	193	61	49	55	162	88	90	89	104
70	0100–0115	0	Stars and cloud	10	29	15	22	185	39	19	29	181	30	66	48	213
71	0410–0425	0	Clear	10	—	35	35	49	—	41*	41	22	—	85*	85	41

Calanus finmarchicus — Stage IV

Expt. no.	A	α	A+α/2	n
61	76	25	50·5	37
62	10	21	15·5	116
63	51	43	47	103
64	23	46	34·5	110
65	45	36	40·5	170
66	43	50	46·5	84
67	2	3	2·5	503
68	35	10	22·5	124
69	43	40	41·5	195
70	21	14	17·5	124
71	—	—	—	—

Calanus finmarchicus — Stage V

Expt. no.	A	α	A+α/2	n
61	63	30	46·5	47
62	12	31	21·5	202
63	43	33	38	156
64	30	41	35·5	141
65	48	45	46·5	122
66	23	41	32	105
67	15	12	13·5	370
68	34	21	27·5	175
69	32	26	29	172
70	20	19	19·5	138
71	—	—	—	—

Pseudocalanus elongatus — Males

Expt. no.	A	α	A+α/2	n
61	—	—	—	—
62	—	—	—	—
63	—	—	—	—
64	—	—	—	—
65	—	—	—	—
66	—	—	—	—
67	7	5	6	135
68	15	45	30	56
69	21	28	24·5	62
70	22	16	19	60
71	—	24*	24	17

Pseudocalanus elongatus — Females

Expt. no.	A	α	A+α/2	n
61	—	—	—	—
62	5	27	16	140
63	38	31	34·5	307
64	44	35	39·5	146
65	49	53	51	313
66	33	26	29·5	100
67	47	73	60	489
68	34	46	40	103
69	32	40	36	306
70	18	68	43	125
71	—	36*	36	47

Pseudocalanus elongatus — Stage IV

Expt. no.	A	α	A+α/2	n
61	—	—	—	—
62	—	—	—	—
63	—	—	—	—
64	—	—	—	—
65	—	—	—	—
66	—	—	—	—
67	52	44	48	124
68	27	12	19·5	50
69	60	64	62	90
70	4	42	23	123
71	—	50*	50	18

Pseudocalanus elongatus — Stage V

Expt. no.	A	α	A+α/2	n
61	—	—	—	—
62	8	39	23·5	234
63	31	35	33	298
64	30	19	24·5	94
65	55	72	63·5	110
66	52	36	44	62
67	62	52	57	652
68	43	12	27·5	147
69	22	30	26	429
70	18	16	17	290
71	—	32*	32	83

Table 5. *Long-tube experiments (duration 1h) carried out in 1939*

	Expt. 10			Expt. 11				Expt. 12							Expt. 13					
	Plankton in G			Plankton in D				Plankton in A							Plankton in G					
Depth (m)	0–3·5			0–3·5				0–3·5							5–8·5					
Time (G.M.T.)	1612–1712			1050–1150				1151–1251							1405–1505					
Date	30 June			1 July				3 July							3 July					
Weather	Sunny, some cloud, no wind			Sun and haze, light N. breeze				Cloudy							Cloudy with some sun					
	D. gracilis			*D. gracilis*				*D. gracilis*				*C. strenuus*			*D. gracilis*				*C. strenuus*	*Leptodora*
	♀	♂	V	♀	♂	V	III	♀	♂	V	III	V	IV	III	♀	♂	V	III	V	
A	4·2	5·4	0·6	47·3	36·8	55·8	61·5	17·2	6·3	26·3	7·2	26·4	39·0	39·1	22·5	27·1	18·9	8·3	46·9	23·4
B	2·1	6·8	3·8	10·5	8·9	3·8	8·4	13·1	19·4	13·7	13·9	19·8	25·3	9·2	8·3	11·9	3·4	1·7	—	10·6
C	2·1	2·9	—	9·8	12·9	2·9	2·8	16·8	17·4	9·4	15·4	15·7	5·3	19·5	7·8	13·5	7·8	10·1	1·9	8·5
D	2·5	5·0	3·8	4·6	8·6	8·7	10·5	14·0	15·7	9·4	15·4	2·9	10·9	9·2	10·3	9·2	10·7	5·2	9·4	2·1
E	7·6	9·6	3·1	3·7	13·6	4·8	4·9	4·1	7·6	3·5	11·8	4·4	2·8	1·1	6·7	5·3	12·6	13·5	17·5	6·4
F	22·0	27·5	23·9	11·3	9·6	5·8	9·1	19·5	18·7	20·8	21·1	16·5	5·6	3·4	13·0	7·4	9·2	10·9	24·4	4·3
G	59·4	42·8	64·8	12·9	9·6	18·3	2·8	15·1	14·8	16·9	14·9	14·3	11·2	18·4	31·4	25·6	37·3	50·3	—	44·7
Total number	709	280	159	459	280	104	143	819	540	255	194	273	285	87	653	488	206	229	160	94

Table 6. *Duration series of experiments carried out, using the long tube in 1947*

All experiments were made from 0 to 3·5 m with plankton in G

	Expt. 39							Expt. 40							Expt. 41	
uration	30 min							1 min							2 min	
ime	0900–0930							1030–1031							1602–1604	
ate	16 July							16 July							16 July	
eather	Dull, no wind							Dull, no wind							Dull no wind	
	Daphnia hyalina		*Diaptomus gracilis*				*Cyclops strenuus*	*Daphnia hyalina*		*Diaptomus gracilis*				*Cyclops strenuus*	*Diaptomus gracilis*	
	Large	Small	♀	♂	V	IV	V	Large	Small	♀	♂	V	IV	V	V	IV
A	0·7	—	1·0	—	—	—	—	—	—	1·7	—	0·8	0·2	2·8	1·5	—
B	1·0	—	—	—	—	0·3	—	—	2·7	1·2	—	0·8	0·5	1·4	—	—
C	0·7	1·8	—	4·4	0·4	0·9	21·0	—	2·7	1·2	—	—	0·6	0·7	—	0·3
D	3·0	1·8	10·2	19·3	5·4	6·5	22·0	3·0	5·3	1·7	4·0	2·2	1·5	0·7	—	2·8
E	18·7	8·8	17·8	32·4	26·1	18·4	16·0	6·1	—	2·3	1·6	2·6	4·2	9·0	13·4	16·0
F	30·5	34·2	29·6	28·1	26·5	26·6	17·0	34·2	8·0	18·6	20·8	19·1	16·8	31·2	22·4	37·1
G	45·6	53·5	41·3	15·8	41·6	46·8	24·0	56·7	81·3	73·2	73·6	74·6	76·3	54·1	62·7	43·7
otal umbers	305	114	196	114	257	1105	100	164	75	172	125	267	1393	144	67	363

	Expt. 42			Expt. 43					Expt. 44			Expt. 45		Expt. 46				
uration	3 min			4 min					5 min			10 min		20 min				
Time	1704–1707			0907–0911					1400–1405			1643–1653		0930–0950				
ate	16 July			17 July					18 July			17 July		17 July				
eather	Dull, no wind			Dull, no wind					Dull, no wind			Dull, slight breeze		Dull, no wind				
	D. gracilis			*D. gracilis*					*D. gracilis*			*D. gracilis*		*D. gracilis*				
	♀	V	IV	♂	V	♀	IV	III	V	IV	III	V	IV	♂	♀	V	IV	
A	—	—	—	—	—	—	0·6	0·3	—	—	—	—	0·5	0·3	—	0·4	—	
B	—	—	0·2	0·7	0·8	0·7	0·6	—	—	0·7	—	—	0·3	0·3	—	—	—	
C	—	—	0·3	3·7	0·4	2·8	1·6	2·2	2·5	0·7	—	2·1	0·5	3·6	1·9	0·9	0·7	
D	0·8	—	—	—	—	—	—	—	0·8	—	4·1	13·4	10·3	10·9	3·8	2·0	2·8	
E	7·2	4·4	11·8	—	48·8	0·7	0·3	8·5	0·8	0·9	6·2	28·2	25·3	16·6	12·4	6·1	7·5	
F	28·8	21·0	27·1	41·5	43·6	22·5	51·2	26·5	10·8	14·0	15·9	29·6	28·6	38·4	34·9	49·5	30·5	
G	63·2	74·6	60·8	54·1	55·2	73·2	45·5	62·2	85·0	83·6	73·8	26·8	34·3	29·8	46·8	41·2	58·3	
otal umbers	125	248	936	135	259	142	318	635	120	429	145	142	367	302	209	459	1263	

Table 7. *Long-tube experiments carried out in 1947; duration of each experiment, 15 min*

	Expt. 48 Plankton in D						Expt. 49 Plankton in A						Expt. 50 Plankton in G		Expt. 51 Plankton in A		Expt. 52 Plankton in D		Expt. 53 Plankton in G	
Depth (m)	0–3·5						0–3·5						12–15·5		10–13·5		10–13·5		20–23·5	
Time (G.M.T.)	0843–0858						1000–1015						1310–1325		0845–0900		1305–1320		0945–1000	
Date	22 July						22 July						22 July		23 July		23 July		29 July	
Weather	Broken clouds, lake flat						Broken clouds, lake flat						Broken clouds, lake flat		Dull, slight drizzle		Dull, rain			
	Daphnia hyalina	*Diaptomus gracilis*				*Cyclops strenuus*	*Daphnia hyalina*	*D. gracilis*			*Cyclops strenuus*		*D. gracilis*		*D. gracilis*		*D. gracilis*		*D. gracilis*	
	Small	♀	♂	V	IV	V	Small	♂	V	IV	IV		V	IV	V	IV	V	IV	V	IV
A	1·2	2·2	1·0	0·9	—	3·8	51·4	32·4	11·9	25·7	51·2		11·1	4·5	55·0	49·8	24·2	24·7	5·0	2·9
B	—	13·5	5·8	11·0	10·1	3·8	8·6	28·2	26·7	33·0	26·7		15·1	15·4	20·0	20·1	14·5	19·2	6·7	3·3
C	28·8	14·6	16·5	14·8	16·5	21·8	5·7	15·5	21·8	13·8	5·8		12·7	23·7	5·0	17·0	17·7	20·6	10·0	6·5
D	51·2	39·3	58·3	51·5	37·1	29·5	14·3	9·9	15·8	5·5	9·3		19·8	29·5	8·3	5·5	12·9	17·1	16·4	15·0
E	7·5	14·6	9·7	10·4	13·3	—	11·4	11·3	6·9	12·9	3·5		21·4	16·4	6·7	4·0	16·1	7·5	15·9	19·4
F	2·5	4·5	1·9	2·2	4·4	9·0	8·6	—	5·9	2·3	2·3		15·1	6·8	3·3	1·6	6·5	5·5	13·2	23·1
G	8·8	11·2	6·8	9·1	18·6	32·0	—	2·8	10·9	6·9	1·2		4·8	3·5	1·7	2·0	8·1	5·5	32·9	29·7
Total number	80	89	103	318	1010	78	35	71	101	218	86		126	602	60	253	62	146	402	613

ON THE BIOLOGY OF THE STONE-LOACH *NEMACHEILUS BARBATULA* (L.)

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(With 7 Figures in the Text)

The stone-loach, *Nemacheilus barbatula* (L.), has a wide range in Europe and Asia. In the British Isles, it occurs nearly everywhere except possibly in the north of Scotland where it was recorded by Day (1880–84) but not by Regan (1911). It can tolerate a wide range of environmental conditions: it has been found from near sea-level (in southern rivers) to over 1000 ft (e.g. Malham Tarn, 1229 ft), in soft and hard waters, in still and flowing water, under ice, and in water at 21° C.

The present study was made on stone-loach from the Lake District, particularly in the Windermere area (Fig. 1). Here I have found it in rivers and streams, but never above the first waterfall; on lake shores, it is rare. No stone-loach have been found, for example, in either Windermere or Coniston Water and only one specimen in Rydal Water. The only place in a lake where I have found the fish plentiful is a stretch of shore about 100 yd long at the head of Esthwaite Water; it occurs nowhere else in this lake. Near this stretch of shore is the mouth of Black Beck, one of Esthwaite Water's main inflowing streams, in which the fish is abundant. The first 600 yd of Black Beck have been deepened artificially; in this stretch which has a muddy bottom with few stones I have never seen or caught the fish, although there is no physical barrier to prevent the fish from migrating from the lake into the beck. These two places, the stretch of shore in Esthwaite Water and in Black Beck excluding the first 600 yd, have been my main sources of material. In other rivers and streams in the district, collections show that the fish is locally distributed, often absent where it might be expected. No explanation of its rarity on lake shores has been found.

COLLECTION AND EXAMINATION OF MATERIAL

Collections were made between March 1948 and July 1950. No definite collecting routine was followed except to aim at securing at least one collection of not less than 20 fish in each calendar month.

The method of capture was determined by the behaviour of the fish, which in daylight lies dormant beneath stones and only becomes active in darkness. If a stone is lifted gently, some seconds elapse before the fish moves, the time interval being longer in still than running water. Once active, the fish moves rapidly along the bottom, often quicker than the eye can follow, for a short distance, coming to rest either under another stone or in a crevice, or sometimes in the open. To catch the fish, a hand-net was designed with a D-shaped mouth, the straight side of the D lying on the bottom; this net had a mesh which retained all fish over 2·0 cm. In running water, the net was placed across the current, the mouth of the net facing upstream. Stones

Fig. 1. Sketch-map showing places where stone-loach have been found (●) and searched for but not found (×).

immediately above the net were then turned over vigorously by kicking, and after a few moments the net was lifted and any fish removed. This process was repeated at 5–10 yd intervals, the work always being done in an upstream direction. In still water, the technique was essentially the same except that without the current and banks fewer fish were usually caught in a given time. This 'hit or miss' method is likely to have been less selective for size of fish than the alternative one of first seeking an individual fish and then trying to catch it. Even so, there may have been some selection, for apparent differences in behaviour of small and large fish when disturbed were observed. On fine days in spring and summer, when the fish could be easily seen, a visual estimate suggested that the ratio of small to large fish was greater in the water than in the net at the time; this visual impression was confirmed later from age-group analysis. Age-group analysis showed, in addition, a greater disproportion between the expected ratio of small to large fish in collections from the beck than from the lake, a difference which suggests that moving water may be an additional factor favouring capture of large fish, perhaps because such fish present a greater surface area to the current. These observations on the behaviour of the fish in Black Beck and Esthwaite Water, arising from the collecting technique, were used to assess the relative populations of stone-loach in other waters.

A total of 780 stone-loach was collected from all sources: 229 from Esthwaite Water, 413 from Black Beck, 76 from Blelham Fish-Pond Beck, 26 from the River Brathay, 25 from the River Rothay and 11 from the River Kent. In addition to this Lake District material, data on length, weight, sex and food of 27 stone-loach from Malham Tarn have been obtained.

All fish were examined fresh. Total length was measured in millimetres from the tip of the snout to the end of the caudal fin, which has no fork. After removal of excess moisture each fish was weighed to the nearest milligram. In a few instances, the length of the pectoral fin and certain body measurements were taken to see if such data could be used to identify sex by external examination alone. Sex and state of gonad were noted by internal examination, and the gonad was weighed if mature. Otoliths and stomachs were removed for study of age and food respectively.

HABITS AND MOVEMENTS

The stone-loach is a poor swimmer, though when disturbed it can move swiftly over short distances, always along the bottom. Although swift currents do not prevent it from moving upstream, I have usually found it where the current is not at its strongest. Distribution is not however noticeably affected by surface velocities because the fish spends much of its time beneath stones on the bottom. By night or on dark days, the fish may be seen resting on the bottom and occasionally swimming actively to the surface, but on fine days it lies in an apparently dormant state under stones. The character of the bottom is evidently unimportant in the ecology of the fish as I have found it on sandy, gravelly and muddy bottoms. Regan (1911) noted that it generally occurred in small clear streams with sandy or gravelly bottoms. Day (1880–84) observed that it browsed among long floating grass quite as commonly as under stones and that in rivers in flood or where very muddy, it sought refuge at the sides under

backs. Foster (1884) quotes Lankester that in the Hitchin district 'the fish lie concealed under stones and weeds all the summer, but in March may be seen lying in the shallows in numbers'.

The behaviour of the fish when feeding was described 40 years ago by Bateson (1890) who says that stone-loach feel for food with their barbels. It never starts 'in quest of food when it is first put into a tank but waits for an interval doubtless until the scent has been diffused through the water. They then swim vaguely about and appear to seek it by examining the whole area pervaded by the scent, having seemingly no sense of the direction whence it comes.' That the fish does not feed by sight is evident both from the position of its eyes on the dorsal surface of the head and its behaviour when feeding.

The fish is not solitary in habit, two or more fish being commonly found under the same stone, which is often shared with minnows (*Phoxinus phoxinus*) and young trout (*Salmo trutta*). Large gatherings of loach, such as those of *Nemacheilus mokokchus* described by Hutchinson (1888), who saw 200 or more in a mountain pool in northern Tibet, have not been recorded in Britain. Moreover the few instances of large aggregations of stone-loach of which I know, occurred in polluted waters and not the clear gravelly streams often referred to as characteristic habitats of the fish. Both Black Beck and the locality in Eskdale Water from which most of my material came receive organic pollution, the former the sewage from a small town, the latter from cattle. Mr R. S. Fort of the Lancashire River Board has told me that on two occasions when he found large numbers of the fish, the water had been polluted with organic matter. On the other hand Lankester (1849) noted an upstream migration of the fish in January which he believed was a movement away from pollution downstream. In a trout stream which had been polluted with organic matter Mr Fort tells me that he found no fish immediately below the affected place, then a stretch where stone-loach were numerous, and further downstream still stretches where stone-loach together with trout were present. This observation suggests that stone-loach can tolerate higher levels of pollution than trout.

GENERAL FEATURES

A general description of the biology of the fish can be found in Day (1880–84) and Regan (1911). A few additional observations on sexual dimorphism and length–weight relationship will be given here.

In many fish the pectoral fin is relatively long and pointed in the male and round and short in the female. Measurements to define this relationship more precisely (Fig. 1) showed that when the length of the pectoral fin was related to three body measurements, a difference, which was statistically significant, was apparent between the lengths of male and female fish. In most adult fish, but not all, the male pectoral fin was longer than that of the female: the distinction is therefore a useful but not infallible means of determining sex from external examination. Immature fish could not be separated in this way. Similar measurements by Vladykov (1928) showed clear-cut differences between adult males and females caught in the same place: owing to variations in size, however, the distinction was no longer true if fish from

different places were grouped. The greater length of the adult male pectoral fin has been noted also by Oliva (1952).

In the breeding season, no change of colour in either sex has been seen but small papillae, present on the pectoral fins of only male fish, have been found. These papillae, described by Vogt & Hofer (1909) and also Vladykov (1928), who found them only in the male, are, according to Vladykov, a constant character of fish over 80 mm long, independent of the breeding season, and are always absent from the female.

Regan gives the mean length of the fish as 3–4 in. (7·6–10·2 cm), maximum length about 5 in. (12·7 cm), which correspond quite well with my own data on length of fish of more than a year old from the Lake District. In Scandinavia and western and northern Europe the fish never seems to attain more than 10–13 cm (Smitt 1892).

The length–weight relationship of 246 mature male and 178 mature female fish has

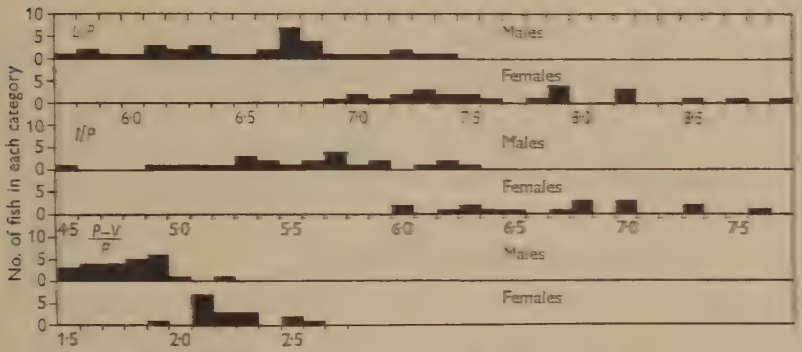

Fig. 2. Frequency distribution showing, in each sex, the ratio of the length of the pectoral fin to three body measurements. *L*, length of body (snout to end of caudal fin); *l*, length of body (snout to caudal peduncle); *P*, length of pectoral fin; *P*-*V*, length between anterior margins of pectoral and pelvic fins.

been analysed statistically. Regression equations of the type $Y = AX^b$ (where Y = weight in grams, A = a constant, X = length in centimetres and b = the slope of the line), or in logarithmic form $y = a - bx$ (where $y = \log Y$, $a = \log A$ and $x = \log X$) were calculated. The data were subdivided according to season and place of capture. It was found that regression coefficients in neither sex differed significantly from 3 (for males, $b = 2{\cdot}98$, S.E. $\pm 0{\cdot}03$, and females, $b = 3{\cdot}05$, S.E. $\pm 0{\cdot}05$), thus the length–weight relationship for both sexes agrees with the cube law. The coefficient 3 was used accordingly in calculating adjusted mean weights. No significant differences in the slope of the regression line of male fish were found either according to habitat or season. The only group of female fish in which the slope of the line (b) differed significantly from 3 was that of spent fish caught in July and August; this group had a wide scatter about the regression line ($b = 2{\cdot}65 \pm 0{\cdot}13$). Adjusted mean weights, which give a comparison of weights of fish of the same length at different times of year, were calculated for each season for males and females separately. These figures show that in both sexes, the lowest figures of the percentage of the mean weight occur in the period from November to February, 94% for males and 89% for females. Mature females before spawning have a figure of 104%, while in spent females in

July and August, this figure is almost as high, 101%; by September–October this figure for spent females has fallen to 93%. This gradual fall instead of the sharp drop which might be expected as a consequence of shedding ova at the breeding season is in keeping with the observation that not all the eggs are shed at spawning and that a variable proportion may be retained and presumably reabsorbed later.

PARASITES AND PREDATORS

Nearly all stone-loach have internal parasites, none of which have been identified. Small nematodes frequently occurred in the liver, gonad or body-cavity. Occasionally, trematodes were found in the head and probably emerged from the eye-capsules, damaged in extraction of otoliths. In two fish, adult tape-worms were found in the body cavity; the weight of one of these cestodes was 0·9 g or 10% of the body weight of the fish.

I can add nothing to what is already known about predators. Bolam (1913, p. 25) records a trout caught on the River Lliw which was gorged with the fish, and Watson (1925, p. 201) mentions eels as predators. Hartley (1948) found stone-loach in the stomachs of pike and eels from the River Cam. The many references to its effectiveness as a bait for trout and eels indicate that these observations are not isolated instances. Birds and mammals also eat the fish. A dipper has been seen killing a stone-loach (Bolam 1913, p. 381), the stomach of a greenshank killed on the River Irving in Cumberland contained 15 stone-loach (Johnson 1918) and the otter is cited by Watson (1925) as a predator.

In addition to death from natural causes, an observation of some practical value concerning stone-loach which died in an aquarium may be mentioned: at and above 0·20 p.p.m. of copper (Cu^{++}) the fish died within 24 h (Mackereth & Smyly 1951). F. J. H. Mackereth determined the copper in Black Beck in June 1951 as 0·13 p.p.m. Cu^{++} and in the experimental tank in which the fish died as 0·27 p.p.m. Cu^{++}.

AGE AND GROWTH

Age was determined from otoliths; these bones were extracted through the ventral surface of the skull, a method both quicker and more certain than the conventional technique of taking a horizontal slice off the dorsal surface of the head. Some otoliths were mounted permanently in Canada balsam, but the majority were stored dry in specimen tubes from which they were easily removed with a moist brush when required. When otoliths were immersed for a few minutes in pure creosote oil and then examined by reflected light against a dark background, alternate translucent and opaque rings were visible. With few exceptions, the rings of both otoliths from the same fish were identical in number and arrangement. In many large fish, the ring structure of the otolith was more clearly seen after some excess bone had been removed by grinding, as has been done with eel otoliths (Frost 1945).

It was deduced that the ring structure of the otoliths was annual in character on two grounds. First, a marked change in the structure of the otolith was observed at only one season of the year; secondly, when the otoliths of fish caught in the same month were grouped according to the distribution of length shown in Fig. 3, it was found

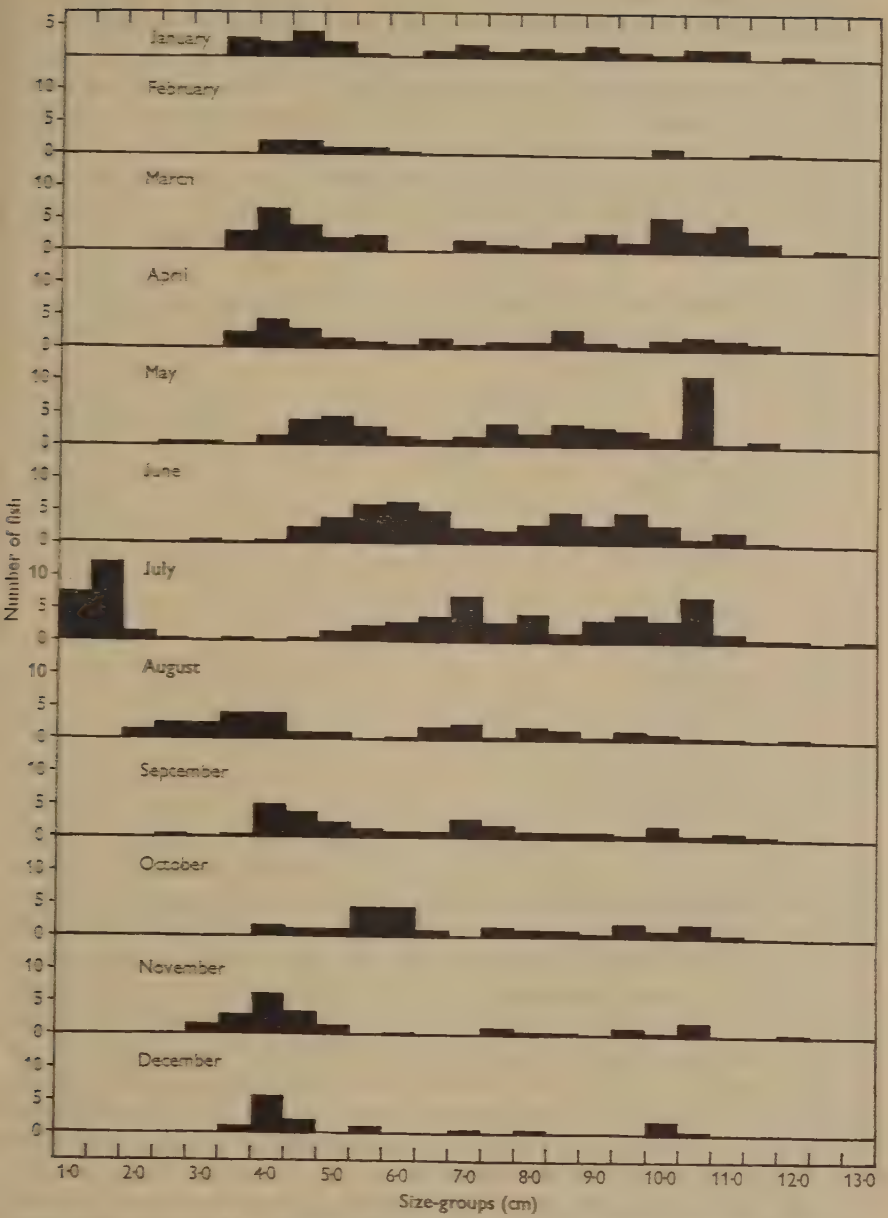

Fig. 3. Distribution of length among 780 stone-loach caught by hand-net in the Lake District between March 1948 and July 1950.

that otoliths of fish in the length range 0–6·0 cm, which are first seen as a distinct group in July and can only be fish in their first year of life, were distinctly different in structure from those of all longer fish. In fish less than 6·0 cm, the otolith was a round opaque disk, elliptical in cross-section, but in fish more than 6·0 cm, the otolith was a central opaque plate surrounded by one or more pairs of concentric rings, each such pair composed of an inner translucent ring and an outer opaque ring. In most fish, the peripheral opaque ring was narrow at only one season of the year, May and June; a small number of fish had it in April and in a few of the largest, and presumably oldest, fish it was seen in July, August and September. The occurrence of this thin

Table 1. *The mean length of fish which have* (*N*) *a narrow opaque ring or* (*W*) *a wide opaque ring on the edge of the otolith, subdivided according to the total number of opaque rings on the otolith*

Number of opaque rings		April		May		June		July	
		N	W	N	W	N	W	N	W
0	Mean length	.	4·8	.	5·4	.	.	1·7	.
	Number of fish	0	28	0	29	0	0	44	0
	Increment	.		.		.		.	
1	Mean length	.	8·3	5·2	8·3	5·8	8·8	6·7	.
	Number of fish	0	1	6	11	49	4	38	0
	Increment	.		3·1		3·0		.	
2	Mean length	8·3	9·6	8·5	10·2	8·4	9·6	8·6	.
	Number of fish	4	12	7	23	27	5	32	0
	Increment	1·3		1·7		1·2		.	
3	Mean length	10·6	11·1	10·5	11·0	10·1	.	10·4	.
	Number of fish	1	5	6	6	12	0	17	0
	Increment	0·5		0·5		.		.	
4	Mean length	.	11·3	10·7	10·9	11·2	.	11·3	.
	Number of fish	0	2	1	2	5	0	7	0
	Increment	.		0·2		.		.	

narrow opaque zone on the edge of the otolith at only one season of the year suggested that it was very probably annual in character; this supposition was checked by calculating the mean lengths of fish within the same ring-group which had either narrow or wide marginal opaque rings, the argument being similar to that of Hartley for the roach (1947). Table 1 shows the relevant data for April to July. Except for ring-groups 3 and 4 in which increment in length through the year is very small, maximal length in each ring-group occurs in May and June. At this season also the figures show a decrease in length because fish which have acquired the narrow opaque marginal ring are promoted thereby into the next higher ring-group. These facts can be explained rationally only if the rings are formed annually. A few otoliths showed checks not of an annual character (false rings), but these could be distinguished from the annual rings by their discontinuity and lack of sharp definition, features clear to the experienced eye but difficult to define in writing. For convenience it is assumed that the fish complete each year of life on 31 May and each age-group is numbered consecutively in Roman numerals from 0 to V.

Table 2 gives the numbers of fish in each age-group. Comparison of the results from Esthwaite Water and Black Beck shows that whereas in the beck a fair number

of fish attain an age of 4 or 5 years, in the lake, few fish live more than 3 years. Whether this difference in age composition results from greater longevity of fish in the beck or from migration of older fish in the lake into the beck is not known.

Table 2. *Results from age determinations arranged to show the number of fish of each sex in each age-group*

	Age-group						
	0	I	II	III	IV	V	Total
Esthwaite Water							
Males	27	30	30	3	0	0	90
Females	33	24	12	3	0	0	72
Sex unknown (immature)	56	1	0	0	0	0	57
Total number of fish	116	55	42	6	0	0	219
Black Beck							
Males	34	48	65	21	9	1	178
Females	53	36	37	26	12	1	165
Sex unknown (immature)	62	0	0	0	0	0	62
Total number of fish	149	84	102	47	21	2	405
Other stations							
Males	25	20	13	3	0	0	61
Females	28	17	9	9	4	3	70
Sex unknown (immature)	3	0	0	0	0	0	3
Total number of fish	56	37	22	12	4	3	134
All Stations							
Males	86	98	108	27	9	1	329
Females	114	77	58	38	16	4	307
Sex unknown (immature)	121	1	0	0	0	0	122
Total number of fish	321	176	166	65	25	5	758

Length for age of stone-loach in the Lake District is shown in Table 3, where it will be seen that although in early life growth is on the average relatively fast, individual growth-rates vary considerably, some fish attaining only 3·0 cm after 12 months and others reaching 6·5 cm in 6 months. Growth-rate diminishes in age-group II and practically ceases in older fish.

Fig. 4 shows the length and weight attained by each age-group in Esthwaite Water and Black Beck. It will be seen that, after the first 2 years of life, fish in the beck grow faster than fish in the lake. This difference in growth-rate of fish in age-group II suggests some local environmental difference between the two localities. It was noted earlier that the collecting place in Esthwaite Water is the only lake shore where the fish has been found; as only 600 yd separate the two collecting places, it may be that some fish from the beck have found conditions at this single locality where they can live though not grow so fast after the first year of life; whether they also have a shorter life or do not remain in the place longer than 3 years is not known.

In Fig. 4 the data have been arranged in quarterly groups so as to show seasonal as well as annual changes in growth-rate. In age-groups 0 and I it will be seen that in both lake and beck increase in length and weight is large between June and November but small between December and May. In the beck fish in age-group II maintain this pattern of growth, but in the lake they do not. Analysis by the '*t*' test shows that the differences in both length and weight of lake and beck fish are highly significant in

age-group II and in all subsequent age-groups in which there are enough fish for statistical analysis. Visual examination of the slope of the curves suggests that even in age-group I the fish in the beck attained a greater length for age than fish in the lake.

The growth-rate of stone-loach in other streams and rivers in the Lake District resembles that of the fish in Black Beck, though the scanty material does not permit close comparison. No difference was found between the growth-rate of male and female stone-loach in any Lake District waters.

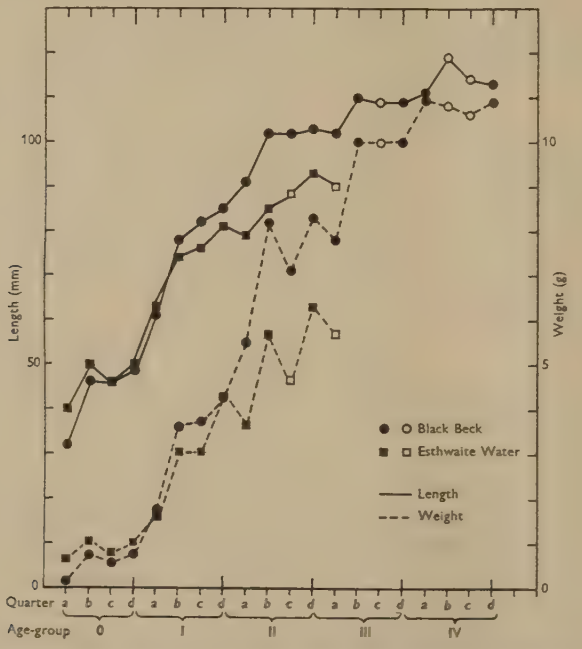

Fig. 4. Mean length in each quarter of 219 stone-loach from Esthwaite Water and 405 from Black Beck, and mean weight of 215 fish from Esthwaite Water and of 389 from Black Beck. Open circles and squares represent means based on fewer than five fish.

FOOD

As would be expected from the habits of the fish, the food was principally invertebrate bottom fauna. Chironomid larvae were a major item of food, but aquatic larval or nymphal stages of several insect groups and adults of some Crustacea were eaten also. No attempt was made to identify the chironomid larvae; other Diptera larvae were grouped as 'Diptera larvae miscellaneous' and among them *Simulium* was often recognized. Aquatic nymphs of Ephemeroptera, and larvae of Plecoptera and Trichoptera were grouped as such and among them the following genera, *Chlöeon*, *Centroptilum*, *Caenis* and *Leptophlebia* (Ephemeroptera); *Perla* and *Protonemura* (Plecoptera); *Stenophylax* and *Hydropsyche* (Trichoptera), were identified. Crustacea which were

Table 3. *Age and length distribution of 772 stone-loach from all Lake District stations*

The numbers of fish in each age and length group are shown subdivided according to the season of capture as follows: *a* = June, July and August; *b* = September, October and November; *c* = December, January and February; *d* = March, April and May.

Length	0				I				II				III				IV				V			
(cm)	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
1·0	15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1·5	24	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2·0	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2·5	6	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3·0	5	3	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3·5	9	7	8	11	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
4·0	8	25	20	25	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
4·5	2	17	16	22	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5·0	2	10	7	16	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5·5	.	11	5	10	17	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
6·0	.	11	1	4	20	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
6·5	.	3	2	4	20	1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
7·0	.	.	.	2	15	6	5	2	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
7·5	.	.	.	1	4	8	2	10	7	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
8·0	.	.	.	.	4	3	3	6	14	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.
8·5	.	.	.	.	2	3	2	8	10	2	0	7	4	.	.	.	.	.	.	.	.	.	.	.
9·0	.	.	.	.	.	.	1	3	10	2	3	9	2	1	.	.	.	.	.	.	.	.	.	.
9·5	.	.	.	.	.	.	.	.	11	3	2	9	8	0	.	.	.	.	.	.	.	.	.	.
10·0	.	.	.	.	.	.	.	.	4	8	6	8	8	1	1	6	1	.	.	.	.	.	.	.
10·5	.	.	.	.	.	.	.	.	2	3	2	23	11	2	1	8	3	.	1	3	1	.	.	.
11·0	.	.	.	.	.	.	.	.	.	3	.	3	3	2	2	6	5	.	1	4	.	1	.	.
11·5	.	.	.	.	.	.	.	.	.	.	.	.	0	1	.	3	2	1	1	3	.	.	.	1
12·0	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	1	.	1	.	.	.	.	.
12·5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
13·0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
Totals	77	88	59	97	106	23	13	29	68	24	14	60	37	8	4	23	12	1	4	10	2	1	0	2
Mean lengths	2·6	5·0	4·7	4·9	6·4	7·7	8·0	8·3	8·7	9·9	9·9	10·1	10·2	11·1	10·8	10·9	11·2	11·8	11·4	11·4	12·2	11·5	—	12·5
S.D. of mean lengths	1·2	0·6	0·5	0·9	1·0	0·8	0·6	0·6	1·0	0·9	0·7	0·8	0·8	0·8	0·3	0·5	0·5	—	0·5	0·3	—	—	—	—

identified consisted of *Gammarus* (Amphipoda) and several species of Cladocera, e.g. *Chydorus sphaericus*, *C. globosus*, *Alona affinis*, *Eurycercus lamellatus*, *Peracantha truncata* and *Sida crystallina*. Ostracoda, Harpacticoida and Copepoda were noted but only one copepod, *Cyclops* (*Eucyclops*) *agilis*, was identified. Food items of rare occurrence belonged to the Annelida (Oligochaeta and Hirudinea), Odonata, Neuroptera, Coleoptera, Hemiptera and Mollusca, among which the genera *Glossiphonia* (Hirudinea), *Sialis* (Neuroptera) and *Pisidium* (Mollusca) were identified. Oligochaeta were all of aquatic origin; Odonata were all nymphal; Coleoptera were represented by both larvae and adults of aquatic origin; Hemiptera were only twice found in the food, on each occasion as a single specimen of the Corixidae. *Pisidium* (Mollusca) were found only in fish from Malham Tarn. Plant debris, filamentous algae and pebbles occurred in small quantities from time to time.

Table 4. *Number of points allotted to each stomach according to its fullness and the length of the fish*

	Length of fish (cm)		
Stomach	0–6	6–9	9–14
Full	60	80	100
¾ full	45	60	75
½ full	30	40	50
¼ full	15	20	25

Stomachs were removed by slitting the belly of the fish from anus to mouth and cutting off the stomach at the oesophagus and pyloric sphincter. It was not practicable to weigh the small amount of food in each stomach separately, so after noting the fullness of each stomach (to the nearest 25 %) and estimating visually the composition of the food according to a points system, all stomachs in one collection were dried and weighed collectively and this dry weight was expressed as a percentage of the wet body weight of those fish which had fed. Hynes (1950) considers that points systems are better than most arbitrary methods of assessing the composition of the food quantitatively. According to the points method which I have used here the contents of each stomach have been awarded a number of points depending on the size of the fish and the fullness of the stomach as shown in Table 4, where the fish have been divided into three length-groups which correspond quite closely to three age-groups, namely 0, I, and II–V respectively. After the preliminary step of deciding on the total points to be given to a stomach, this figure is then subdivided among the component food groups on a visual estimate of their relative volumes. By these methods the food eaten by fish in different places and at different seasons and by fish of different sizes has been compared. The food recorded from the same months in different years showed that the year of capture was unimportant. Owing to small catches of fish in some months, seasonal changes in food and changes in the food associated with size of fish are not given in full; each of these aspects is dealt with separately by grouping data. Data from Esthwaite Water and Black Beck are treated separately. In summarizing either the month-by-month data or size data, the mean number of points awarded to each food item was calculated for each month in each size-group. Monthly means were

then divided by 12 to give data for study of the food of the size-groups, and similarly the means in each size-group were added and divided by 3 to give the data for study of seasonal changes in the food.

Seasonal changes in the quantity of food eaten by lake and beck fish are shown in Fig. 5 where data for all items collectively are given, and in Fig. 6 where data for each item are given separately. In Fig. 5 it will be seen that in winter, both in the lake and in the beck, a minimum of food is eaten, whereas at other seasons there is a maximum

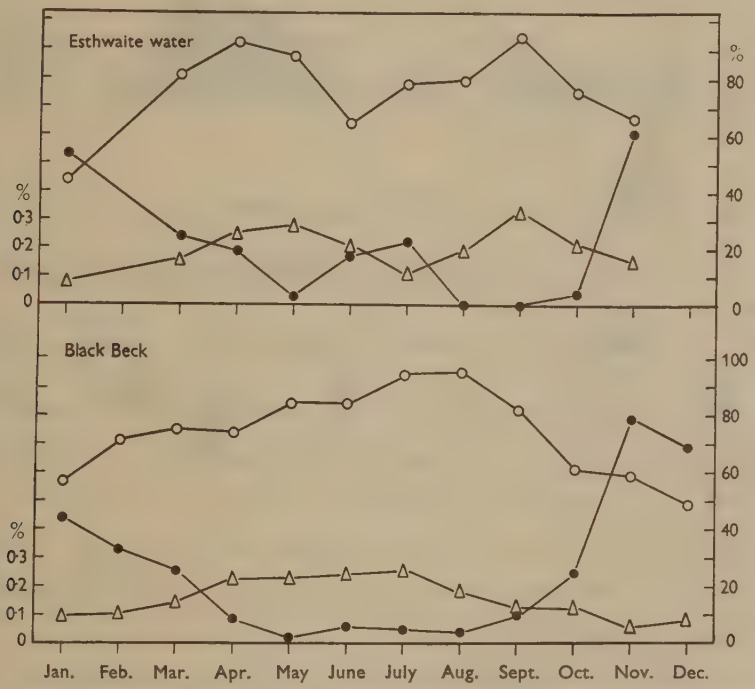

Fig. 5. Seasonal changes in quantity of food eaten by fish in Esthwaite Water and Black Beck. –○–, percentage fullness of stomachs; –●–, percentage of empty stomachs; –△–, ratio dry weight of food : wet weight of fish.

in summer in the beck but maxima in spring and autumn in the lake. Fig. 6 shows that the kind of food is essentially similar in both lake and beck except for the presence of Copepoda, Cladocera and Neuroptera in the food of lake but not of beck fish. There are, however, some contrasts in the extent to which lake and beck fish feed on different kinds of food. Although chironomid larvae are eaten in both localities in all months, in the beck they are the principal food of the fish, whereas in the lake this food item remains proportionately low throughout the year, and other items of food such as Ephemeroptera and Trichoptera larvae, items unimportant to the beck fish, are eaten in equal or greater quantity in spring and early summer. *Gammarus* is eaten by fish in the beck all through the year, though more in winter than in summer, but it is rare in the diet of the lake fish except in July. Among the less common items of food of

lake fish, Copepoda are eaten in small quantity all through the year but Cladocera mainly in the autumn. These differences in the feeding of lake and beck fish probably reflect to a large extent differences in the fauna of the two places.

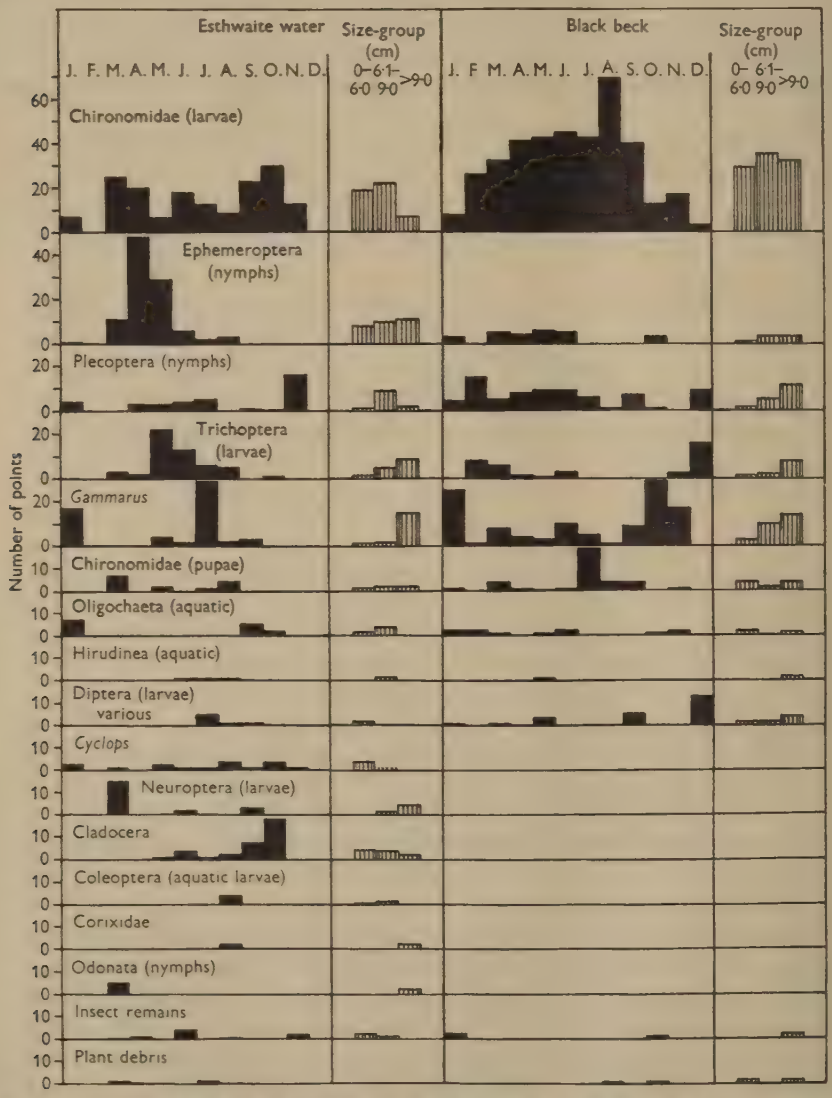

Fig. 6. Composition of the food at different seasons and changes in diet with size of fish in Esthwaite Water and Black Beck. All histograms represent the mean number of points.

Fig. 6 shows also that although all the chief items of food are eaten to some extent by all sizes of fish, there is a tendency for larger organisms to form a larger proportion o the food of larger fish.

Table 5 shows that a similar amount of food is eaten by both lake and beck fish of 0–6·0 cm (which correspond to 0+ age-group fish), but in the beck fish of 6·0–9·0 cm (age-groups I and II) eat more than fish of similar length-range in the lake. This result considered in relation to Fig. 4 shows that in the lake young fish eat as much and grow as fast as young fish in the beck, but older fish (age-group II) eat more and grow faster in the beck than fish of similar age in the lake; there is here a strong probability of a direct association between food and growth-rate.

Table 5. *Amount of food eaten, calculated by the points system, by fish of three sizes according to month and station*

For each size-group the upper figure shows the monthly average number of points allotted to fish from Esthwaite Water, the lower figure the average for fish from Black Beck.

Size-group (cm)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
0—6·0	13	—	33	47	51	45	53	46	53	55	29	—
	27	45	28	40	48	41	53	54	53	55	40	13
6·0—9·0	40	—	66	63	67	54	47	63	80	66	67	—
	60	60	80	77	70	72	80	80	80	50	60	40
9·0—14·0	63	—	100	100	92	56	88	—	—	50	—	—
	51	63	76	76	84	84	96	89	83	43	—	75

A comparison of the food of the fish from three different environments, river, lake, and mountain stream, was made in July and August of the same year (Table 6). The importance of chironomid larvae to the fish is seen from their presence in the food in all six habitats, a feature shown by no other food item. Most of the differences in diet shown probably reflect differences in the available fauna, though the result from the river Kent may be exceptional as only four feeding fish were caught there.

Table 6. *Percentage composition of the food in July and August in different habitats*

	Stream, Black Beck	Rivers			Lakes	
		Rothay	Brathay	Kent	Esthwaite Water	Malham Tarn
Number of feeding fish	20	22	12	4	21	18
Chironomidae larvae	59	19	17	15	36	25
Chironomidae pupae	26	.	.	.	4	.
Plecoptera, nymphs	9	12	38	.	17	.
Trichoptera, larvae	.	.	8	.	16	10
Ephemeroptera, nymphs	.	49	25	65	4	.
Gammarus	7	.	.	.	12	.
Cladocera	.	.	.	21*	1	34†
Mollusca	.	.	.	.	.	12
Miscellaneous	.	20	18	.	10	19

* *Alona affinis.* † *Bosmina* sp.

Comparison of the food of stone-loach with other species of fish is possible for the River Brathay for which water the food of young trout and minnow is also known; the data for these fish (Frost 1943) compared with those of the stone-loach (Table 7) show that the chief food items are eaten by all three species though their proportions differ markedly in some instances, notably in the greater proportion of Plecoptera nymphs eaten by stone-loach than by brown trout fry or minnows.

REPRODUCTION

Sex was determined in all fish by internal examination, the condition of the gonad being classified as immature, ripe, or spent. Immature fish were rather difficult to sex, and of 330 immature fish 129 were classed as sex unknown. The remainder consisted of 92 males and 109 females, a ratio possibly influenced by an immature ovary being slightly easier to recognize than an immature testis. 237 and 212 female fish were sexually mature and one fish was hermaphrodite. The combined totals of immature and ripe fish of each sex was 329 males and 321 females, from which figures it may be concluded that in nature the sexes occur in similar numbers.

Table 7. *Percentage composition of the food of stone-loach, brown trout fry and minnow from the river Brathay*

		Stone-loach	Data from Frost (1943)	
			Brown trout fry	Minnow
Surface insects	aquatic	0	5·6	0·8
	terrestrial	0	8·1	6·5
Chironomidae	larvae	16·5	27·9	15·8
	pupae	0·1	7·1	4·3
Cladocera		0	1·0	1·9
Ephemeroptera, nymphs		25·4	25·4	11·9
Plecoptera, nymphs		37·6	9·7	1·6
Trichoptera, larvae		7·6	12·2	9·3
Diptera, various larvae		8·9	1·0	1·6
Gammarus		0	2·0	0·7
Hirudinea		2·4	0	0

In the Lake District, the fish spawns in May, though some breeding may take place in April and June, and a few ripe females have been found as late as July. These latter fish, however, are probably ones which failed to spawn, as the eggs were duller in colour and less turgid in appearance than eggs of ripe fish caught earlier in the year. Only a proportion of all the eggs in the ovary ripen and are shed at spawning, perhaps half the contents of the ovary remaining immature and unshed.

No eggs were found in the field. In three successive years, fish in an aquarium, in which the water was still, did not spawn; but in a circular concrete pond out of doors supplied with water from jets set at an angle so that the water in the pond was continually moving, captive fish spawned two years running and both eggs and fry were obtained. The eggs from these fish were found scattered over the bottom of the pond, the majority singly. As the spawning act was not observed it is impossible to say whether this distribution of the eggs results from the behaviour of the fish or the movement of the water. The spherical eggs are a dirty white in colour, have a diameter of 1·0 mm and a tough outer skin. The eggs took 14–16 days to hatch in water whose temperature ranged from 12 to 16° C.

The yolk-sac was absorbed within 5–7 days. The eyes are fully pigmented and can be seen through the skin of the egg before hatching. The newly hatched fry measure 3·0 mm in length; the eyes are black and there is a little pigment down the back and beneath the vertebral column internally. By the time the yolk-sac is absorbed the fry

measure 4·0–6·5 mm, the pectoral fins are nearly 1·0 mm in length but without pigment or fin rays, the otoliths are visible and the mouth has as yet no barbels. The fry grow quickly, for the mean length of a sample of 25 fry not more than 5 weeks old was 1·5 cm; one fry, not included in this mean, measured 2·8 cm. By 5 weeks, the barbels have appeared and in this and other characters, the fish resembles the adult in all respects but size. Seasonal changes in the ratio gonad weight: body weight supports the conclusion that May is the month when most fish breed. Only the ovary was used because the weight of the testis (0·05–0·15 g) was seldom more than 2% of the body weight. In Fig. 7 which shows the gonad weight: body weight ratio of mature female

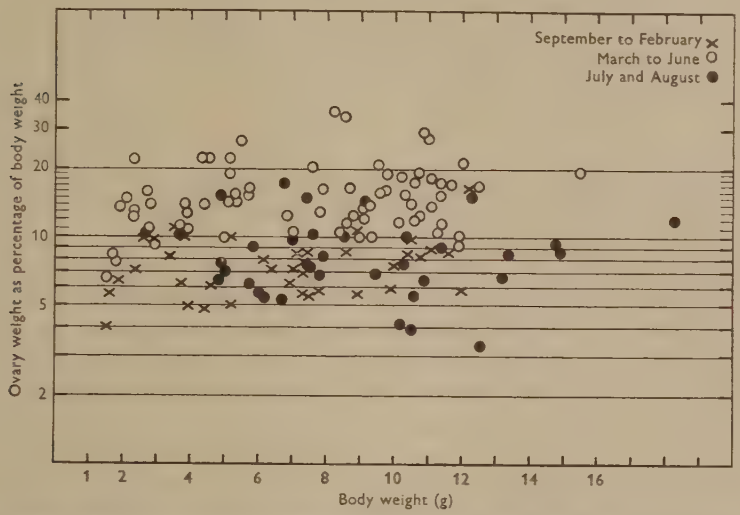

Fig. 7. Relationship between the ovary weight as a percentage of the body weight and the body weight of 144 female stone-loach during three periods of the year, September to February inclusive, March to June inclusive, and July and August.

fish plotted against body weight it can be seen that between September and February this ratio lies between 5 and 10%. From March to June, with a few small fish excepted, this ratio lies on or above 10%, in a few instances reaching the high figure of 35%. From July to August, the ratio ranges between 3 and 20%, the higher values being largely late-spawners or non-spawners. That the ratio does not immediately fall to the autumn and winter level results from the presence in most ovaries of a variable proportion of immature eggs which are presumably slowly reabsorbed. Other writers give the breeding season variously as March (Foster 1934), March and April (Day 1880–84, Yarrell 1836), April and May (Vogt & Hofer 1909) and spring (Watson 1925), statements probably based on observations in latitudes further south where quite possibly the fish spawns earlier in the year. According to observations made near Knopio, Finland, and communicated by W. von Wright to Sundervall (Smitt 1892, p. 713) spawning is at the beginning of June about 14 days after the breaking up of the ice.

The age at which a fish breeds for the first time appears to depend on attainment of a certain minimum size. Individual variation makes it impossible to be exact, but it appears that by December of the year of hatching nearly all fish less than 5·0 cm, and in the following April fish less than 5·5 cm, are immature and will not spawn in the coming breeding season. The number of eggs in the ovary was computed from the eggs counted in a small weighed portion of the ovary. The total number of eggs varied between 5000 and 6000 of which usually rather more than half were ripe; the proportion of ripe to immature was difficult to ascertain visually because there was much variation in egg diameter. There was some tendency for larger fish (over 9·0 cm) to have more eggs than smaller (6·0–9·0 cm) fish; but when body weight was compared with the gonad weight:body weight ratio there was no apparent relationship between the weight of the ripe female and the relative weight of its ovary.

From the observation that the fish remains dormant under stones in daylight and only becomes active after dark it may be assumed with some certainty that spawning takes place in darkness either by night or on dark days. The spawning act has not been observed although attempts were made to observe breeding behaviour. In the spawning season the backs of mature fish are often scratched as if with a pin, which suggests a vigorous rubbing against the under surface of stones. Such action might well accompany spawning.

References in the literature to spawning habits of stone-loach are scanty. Regan (1911) quotes Knauthe (*Zool. Garten.* April 1887), who described how a dozen loach circled round in a deep hole, 'the smaller weaker males following the larger stronger females. Suddenly all the fish darted to the bank, where they squeezed themselves between the projecting roots of an over-hanging tree shedding ova and milt at the same time.' Vogt & Hefer (1909) state that in the spawning act males and females come to lie on their sides belly to belly, so that the reproductive openings are close together and fertilization is made more certain. According to these authors the eggs are not laid in holes but on stones and plants. Hutchinson (1939), commenting on remarkable aggregations of *Nemacheilus stoliczkae* in rivers of northern Tibet, concludes that 'though a solid object forms a nucleus of aggregation, such behaviour is not determined by food', and quotes Hora who considers these aggregations to be, at least in part, expressions of breeding behaviour.

ACKNOWLEDGEMENTS

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SUMMARY

1. The stone-loach (*Nemacheilus barbatula* L.) is locally distributed in the vicinity of Windermere, mainly in the lower reaches of rivers and streams and is usually absent from lake shores.

2. Material for this investigation came from a stream, Black Beck, and a lake, Esthwaite Water. Collections at these two stations were made at monthly intervals from November 1948 to July 1950.

3. External and internal characters including those which distinguish the sexes and some observations on behaviour and movement of the fish are described. The fish is nocturnal, lying dormant under stones in daytime. Field observations suggest that the fish is tolerant of organic pollution.

4. Age has been determined from otoliths supported by length–frequency data. Fish which have attained 2 years grow faster in the beck than in the lake, a difference probably associated with food, as fish over 2 years old in the beck eat more than fish of similar age in the lake.

5. The mean length, in cm, attained at the end of each year of life is as follows: 4·7 (0), 8·0 (I), 9·9 (II), 10·8 (III), 11·4 (IV) 11·5 (V). For the first 2 years of life fish in Esthwaite Water and Black Beck grow similarly, but in the third year of life, fish in Black Beck grow significantly (statistically) faster than fish in Esthwaite Water. Male and female fish grow at a similar rate throughout life.

6. The food, which consists chiefly of chironomid larvae, varies with size of fish, season of year, and place of capture. The amount of food eaten seasonally in Esthwaite Water and Black Beck showed a winter minimum at both stations, but whereas in Black Beck there was a summer maximum, in Esthwaite Water there were maxima in spring and autumn.

7. Spawning takes place in May in the Lake District. Some fish attain 5·0 cm by the winter of their first year of life and spawn when 1 year old; others less than 5·0 cm do not spawn until the next season.

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THE ECOLOGY OF SOME BRITISH SPHAEROCERIDAE (BORBORIDAE, DIPTERA)

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(With 5 Figures in the Text)

Adults of the family Sphaeroceridae are small flies occurring in humid places, numbers being found on the dung of various mammals. Richards (1930) classified the habitats of the family and recorded twenty-nine species as frequenting dung in Britain, of which fifteen were found to be especially coprophilous. Other habitats noticed were decaying vegetation, seaweed, fungi and grass, fermented sap, carrion and the runs and nests of small mammals and birds.

Several species belonging to this family were found to be attracted by pats of cow dung lying on the open field at Rothamsted Experimental Station, Harpenden, Herts. The cow pat lying naturally on the field is a discrete habitat (microhabitat of Mohr, 1943) in which live a well-defined community of dipterous larvae, Collembola, Coleoptera, Acarina and earthworms, as well as smaller organisms (Laurence 1954). Elton (1946) has suggested that there is a strong tendency for species in the same genus to be distributed in different habitats, or to be unable to co-exist permanently in the same habitats. This appears to be opposed to Williams's demonstration (1947) that in a small or simple community there is selection in favour of more than one species in the same genus, rather than in favour of single species in different genera. It was therefore of interest to see how the different species of Sphaeroceridae, belonging to three genera, behaved on the pats of dung.

METHODS

The Sphaeroceridae are most suitable for the study of habits of both adults and larvae of coprophilous insects as the adults tend to live associated with the pat in which the larval stages are developing. The adults live on the surface of, or under, the pat, or in beetle burrows in the pat. The adult flies are difficult to disturb on the dung as they do not readily fly, and they can be collected from the surface of the pat in small glass tubes. If the tube is placed over the flies on the pat surface they normally run up to the top of the tube and can then be shaken into another tube of alcohol. Collections in this way were made from pats of known age (Laurence 1954) from October 1950 to September 1951. As many adults as possible were collected in about five minutes from each pat; by then very few flies were found. It is believed that this five-minute collection of adult flies made a relatively small difference to the number of eggs laid on the pat. For example on 11 July 1950, fifteen females of *Limosina lugubris* Haliday were collected from fresh pats at 10.30 a.m. and at 11.30 a.m. twenty-eight females were collected on the same pats. Also all the flies on the pat cannot be collected in the five minutes, as some retreat into the surrounding grass or beneath the pat. No

collection of adults was attempted in December 1950 as the field was covered by snow for most of the month.

During the period in which adult flies were collected larvae were obtained from the pats by taking four 1 in. cores of dung from each pat and washing out the larvae in

Table 1. *Total adult sphaerocerids collected on cow pats, October 1950 to September 1951*

The nomenclature is that of Richards (1930).

	Males	Females	Total
Genus *LIMOSINA*			
scutellaris Hal.	260	755	1015
crassimana Hal.	335	357	692
lugubris Hal.	404	498	902
silvatica Mg.	11	103	114
collini Richards	86	81	167
pseudoleucoptera Duda	27	36	63
spinipennis Hal.	8	10	18
ferruginata Stenh.	3	10	13
pusilla Mg.	6	2	8
fontinalis Fall.	5	2	7
aterrima Hal.	2	3	5
quadrispina Laurence	2	2	4
rufilabris Stenh.	1	3	4
moesta Villen.	—	3	3
denticulata Duda	1	2	3
atoma Rdi.	2	1	3
vitripennis Zett.	1	3	4
vagans Hal.	1	1	2
humida Hal.	—	1	1
appendiculata Villen.	—	1	1
mirabilis Collin	—	2	2
flaviceps Zett.	—	1	1
sp. nov.*	1	—	1
sp. nov.†	—	1	1
sp. indet.	—	1	1
Genus *COPROMYZA*			
nitida Mg.	21	39	60
hirtipes R.-D.	208	116	324
similis Collin	97	62	159
equina Fall.	32	22	54
roserii Rdi.	—	1	1
pallifrons Fall.	2	1	3
vitripennis Mg.	—	1	1
Genus *SPHAEROCERA*			
subsultans L.	20	15	35
nitida Duda	3	6	9
vaporiarorum Hal.	2	—	2

* Manuscript name *hirticula* Collin.
† Manuscript name *minuscula* Collin.

25% magnesium sulphate solution (Laurence 1954). The larvae were then washed in water and placed on dung from the same pat to continue development so as to determine the species. Adult flies were bred also in 1950 from dung taken from pats in different months during the year and kept in breeding cages.

TAXONOMY

Table 1 gives the numbers of adults of the different species of *Limosina*, *Copromyza* and *Sphaerocera* collected from the cow pats from October 1950 to September 1951. The adults are not difficult to determine using the the keys given by Richards (1930), Séguy (1934) and Duda (1938). The main characters used in separating the species are the wing venation and chaetotaxy of the body. Difficulty has been experienced in defining *Limosina crassimana*. Richards described as a separate species *L. palmata*, which differs from *crassimana* in the length of the prescutellar acrostichal bristles, the length of the mid-metatarsus and its chaetotaxy, and in the presence of a spine-like hair on the cercus of the female. Richards also says that males of *palmata* are difficult to distinguish from males of *crassimana*, having the same genitalia, but are larger and have longer metatarsi. It should be recorded that in *L. crassimana*, in all the specimens I have examined, the metatarsus is slightly longer than the first tarsal

Fig. 1. *a–f*, the anterior spiracles of some sphaerocerid larvae: *a*, *Copromyza nitida*; *b*, *C. hirtipes*; *c*, *Limosina crassimana*; *d*, *L. lugubris*; *e*, *L. silvatica*; *f*, *L. pseudoleucoptera*. *g*, *h*, posterior spiracles of the larvae of two genera viewed laterally: *g*, *Copromyza*; *h*, *Limosina*.

segment and not equal as stated by Richards. All the individuals referred to in this study as *L. crassimana* have long prescutellar acrostichal bristles and all have well developed spines on the mid-metatarsi. Some of the females, however, possess cerci resembling those described for *palmata*, but females of both types have been bred on the same day from the same pat deposited in June 1950. However, Mr J. E. Collin informs me that there are differences in the male genitalia between *L. palmata* and *L. crassimana* and that in his opinion they are separate species. Although the species recorded here as *L. crassimana* may include one or two specimens of *L. palmata*, most may be referred to *L. crassimana*. Hammer (1941) also records difficulty with the determination of *L. crassimana* but believes most of his specimens from cow pats in Denmark are referable to this species. All the specimens recorded as *L. lugubris* appear to be this species and not *L. pseudolugubris*. Hammer (1941) records difficulty in separating *Copromyza similis* and *C. equina*; I have not experienced difficulty in separating these two species. The larvae are maggot-like but differ in the shape of the spiracles (Fig.1).

OBSERVATIONS

Four species of *Limosina* as adults (*L. crassimana*, *L. silvatica*, *L. scutellaris*, *L. lugubris*) were found to be common on the fresh dung and these occurred in the field in succession during the year (Table 2). *L. silvatica* is a larger species and occurs on pats in the winter, in numbers from November until February. *L. crassimana* is a smaller species and is very common from January until April. All *Limosina* adults are rarer in the field in June. *L. scutellaris* appears suddenly and abundantly in May and again becomes

common from July onwards reaching a peak of abundance in September and continuing into October. *L. lugubris* is a summer species, overlapping with *L. scutellaris*, but much more abundant in July and August, becoming rarer when *scutellaris* is common in September. The larvae obtained from the larval sampling carried out between October and September were bred out as adults. The succession of species of larvae present in pats deposited in any month followed the succession of species of adult visitors in those same months, indicating that the adult visitors on the pat are laying eggs in the months in which they are most abundant (Table 3). A similar seasonal succession was observed when breeding flies from dung in 1950.

Seven species of *Copromyza* occurred as adults on the pats at Rothamsted but only three of these lived as larvae in the dung. As in the genus *Limosina* the species differed in their time of appearance during the year. *Copromyza nitida* is a winter species (Table 4). Larvae first appeared in the pats in the field in November and were abundant in December, January and February. Larvae obtained in March were mostly *C. similis*, and they possessed fan-shaped anterior spiracles, resembling those

Table 2. *Seasonal occurrence of* Limosina *adults* (*number per forty pats*), *and the monthly numbers of pats investigated between October 1950 and September 1951*

Peak numbers in heavy type.

	1950			1951								
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.
L. scutellaris	152	11	—	0	0	0	18	**210**	72	124	211	**234**
L. silvatica	0	**40**	—	33	25	2	1	1	0	0	0	0
L. crassimana	14	11	—	65	**120**	93	58	31	14	2	1	23
L. lugubris	28	2	—	0	0	1	16	46	31	245	**415**	100
L. collini	0	0	—	0	0	0	0	0	**55**	50	27	27
L. pseudoleucoptera	0	0	—	0	0	0	0	5	21	0	5	**34**
Monthly numbers of pats investigated:												
Adults collected	28	31	0	21	85	68	104	44	43	47	36	37
Larvae collected	8	22	8	16	22	14	17	10	14	9	11	10

of *C. hirtipes* larvae. The presence of the larvae coincided with the maximum abundance of *C. similis* adults in the field. From April until September *C. hirtipes* was the commonest species, although the numbers decreased during the hottest part of the year when larvae of this species were found principally in the shaded pats. The other species of *Copromyza* found visiting the pats as adults were found not to breed in the dung. Richards (1930) records the common species of *Limosina* and *Copromyza* from a wide range of habitats in most of the months of the year. Their presence in the field on dung only at certain times of the year must depend mainly on the reactions of the adults to the conditions of temperature and humidity obtained in the field at these times.

Two species of *Limosina*, *L. collini* and *L. pseudoleucoptera*, were relatively common on the pats at Rothamsted in the summer (Table 1) but were found more abundantly as adults on older dung. Adults of *L. collini*, *L. scutellaris* and *L. lugubris* occurred at the same time of the year but those of *L. collini* were more abundant later on the pat than adults of *L. scutellaris* and *L. lugubris* (Fig. 2). Larvae of *L. collini* and *L. pseudoleucoptera* possess short anterior spiracles (Fig. 1) and these larvae have been found

only in older pats and not in fresh ones, whereas larvae of *L. lugubris* and *L. crassimana*, which possess long spiracles (Goddard 1938), have been found in pats up to 10 days old and rarely in older pats in June, July and August. In these months fifty-five adult *L. lugubris* have been bred from dung up to 10 days old when it was collected and only one adult *L. collini*, whereas from dung left lying on the field for more than 10 days, eleven adult *L. collini* have emerged and no *L. lugubris*. The absence of adult

Table 3. *The numbers of* Limosina *adults bred from pats in each month, 1950–51*

All pats were lying in the open field; the month is the month of deposition of the pat.

	1950			1951								
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.
L. silvatica	0	20+	8*	32*	32	11	1	0	0	0	0	0
L. crassimana	5	8	0	0	17	66	131†	2	1	1	1	0
L. scutellaris	0	0	0	0	0	0	0	16‡	31	2	1	0
L. lugubris	0	0	0	0	0	0	0	1	30	32§	2	0

* 100%. † 99%. ‡ 84%. § 91%.

L. pseudoleucoptera in July (Table 2) suggests that this species is most abundant early and late in the summer in contrast to *L. collini* which is abundant at the height of the summer. Unfortunately the numbers of adults and larvae of *L. collini* and *pseudoleucoptera* taken on or in the pats have been small. Hammer (1941) records that *L. aterrima* in Denmark is a species which occurs mainly on the older droppings.

Table 4. *Monthly numbers of* Copromyza, *1950–51*

	1950			1951								
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.
Adult *Copromyza* per forty pats:												
C. nitida	0	22	—	23	10	2	0	1	1	0	0	0
C. similis	7	30	—	4	19	40	4	4	0	0	0	0
C. hirtipes	23	17	—	0	1	5	60	36	33	3	22	30
C. equina	0	13	—	0	7	7	5	0	1	0	0	0
Total *Copromyza* bred from pats:												
C. nitida	—	∞*	∞*	68+*	86*	0	0	0	0	0	0	—
C. similis	—	0	0	0	0	6†	2	0	0	0	0	—
C. hirtipes	—	0	0	0	0	2	58‡	0	(96)§	1	(1)§	—

* 100%. † 75%. ‡ 97%. § In shade.

The numbers of the sexes of the different species of *Limosina* and *Copromyza* found on the dung, and emerging from the dung, are given in Tables 1 and 5. At emergence the numbers of the sexes were approximately equal. On the dung males were rare in *L. silvatica* and *L. scutellaris*. Most mating must take place away from the cow pat in these species. Mating has been observed on the pat in *L. scutellaris* and also in the *L. lugubris* and *L. crassimana*, but not in *L. silvatica*. Males were also rare in *Copromyza nitida* and mating in this species must occur away from the pat. Richards (1930) recorded a preponderance of one sex, mostly female, in several species, and supposed this to be due to a difference in length of adult life between the sexes. He also supposed that it is extremely improbable that the difference is due to differences in habit

between the sexes. In *Limosina scutellaris* there were significant differences in the sex ratio in different months of the year. Early and late in the year males were found commonly, but became rare in the hottest part of the year (Fig. 3). During the warmer months this species was found only on moist dung (Fig. 2). It is suggested that the males require a moister environment than the females and that during the hottest months the males retreat from the open field.

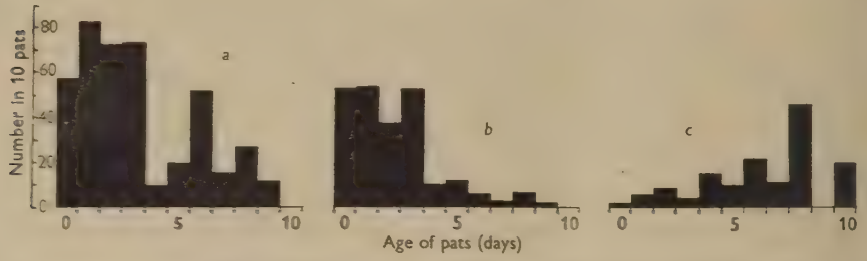

Fig. 2. The succession of *Limosina* adults with ageing of the pat, June to August 1951: *a, Limosina lugubris; b, L. scutellaris; c, L. collini.*

Limosina lugubris lives in the field during the warmest part of the year. Females are capable of flying from pat to pat on hot sunny days as fresh pats are very rapidly colonized (Fig. 4). Males, however, are scarce on fresh pats, but are found abundantly on the same pats on the next day. Between one day and the next there is a night when the humidity is high. If one suggests that males of *lugubris* fly mostly at night then

Table 5. *Sex-ratio of adult sphaerocerids bred from cow pats, January 1950 to September 1951*

	Males	Females	Total
Limosina scutellaris	120	129	249
L. crassimana	266	305	571
L. lugubris	613	566	1179
L. silvatica	75	82	157
L. collini	22	14	36
L. pseudoleucoptera	4	3	7
L. spinipennis	11	11	22
L. pusilla	0	1	1
L. aterrima	2	2	4
L. denticulata	15	14	29
Copromyza hirtipes	41	45	86
C. nitida	52	63	115
C. similis	4	4	8
Sphaerocera subsultans	1	—	1
S. pallidiventris	—	1	1

this could account for the marked differences in numbers of males on fresh and day-old dung. Sphaerocerids are caught in numbers in light traps indicating considerable activity at night. Again it seems probable that the males are more sensitive to low humidities than are the females.

There is no reason for supposing that species breeding in cow dung are restricted to this habitat. *Limosina silvatica* and *Copromyza nitida* emerged from the winter

dung in April, May and June (Table 6), but did not live on the field dung at this time (Tables 3 and 4). Both species must live in a different habitat in the summer. Richards (1930) says that in the Sphaeroceridae in general nearly every species occurs in a wide

Fig. 3. Changes in the sex-ratio through the year of two species of *Limosina* on pats: *a*, *Limosina scutellaris*; *b*, *L. lugubris*. The left-hand column of each pair expresses the number of males as a percentage of the females (right-hand column); the total numbers of both sexes are recorded beneath.

range of habitat. The larvae of the commonest species of *Limosina* (*crassimana*, *lugubris*, *silvatica* and *scutellaris*) were found in field dung from 4 to 50 days old. The dung at this age was sampled for larvae regularly during the year (Table 2) and it is possible to compare the numbers of larvae found in each month with the numbers of adults present in the month the pats were deposited (Fig. 5). At the time when

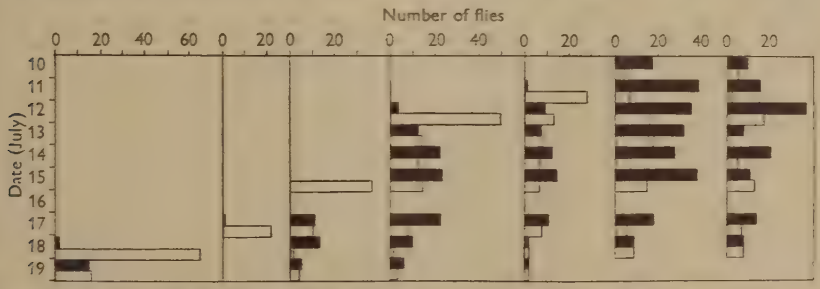

Fig. 4. The succession of adult *Limosina lugubris* visiting pats deposited on seven successive days recorded from 10 to 19 July 1950. Males black, females white.

L. silvatica was in the field up to 90% of the pats were occupied, but the numbers of larvae were relatively small. As the larvae are large this is not surprising. The presence of *L. crassimana* in the field was associated with the significant increase in numbers of larvae in March, when all the pats were occupied. The presence of

Table 6. *Duration of development of Sphaeroceridae (days)*

The month is the month in which a pat was deposited. The duration of development is the interval in days between deposition of the pat and emergence of the adult fly.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Limosina crassimana	—	91–100	58–70	39–65	24–38	21–30	18–25	35	—	—	—	—
L. silvatica	123–141	100–128	79–104	76	—	—	—	—	—	—	205–212	151–176
L. scutellaris	—	—	—	—	29–64	28–42	20–51	36–38	—	—	—	—
L. lugubris	—	—	—	—	27–44	22–33	18–37	29	—	—	—	—
L. denticulata	—	—	—	—	—	34–36	32–45	—	—	—	—	—
L. spinipennis	—	—	—	—	—	28–34	—	—	—	—	—	—
L. collini	—	—	—	—	—	36–50	32–43	—	—	—	—	—
L. pseudoleucoptera	—	—	—	—	68	40	35–44	—	—	—	—	—
L. aterrima	—	—	—	—	—	36	28–35	—	—	—	—	—
Copromyza nitida	109–112	87–107	—	—	—	—	—	—	—	—	196–205	—
C. hirtipes	—	—	60	39–53	22–23	21–23	15	19	—	—	—	—
C. similis	—	—	46–47	47	22	—	—	—	—	—	—	—
Sphaerocera subsultans	—	—	—	—	28	—	—	—	—	—	—	—
S. pallidiventris	—	—	—	—	29	—	—	—	—	—	—	—

L. lugubris in July and August was associated with a similar increase in numbers of larvae. However, when adults of *L. scutellaris* were abundant the numbers of larvae recorded were low, both early and late in the year. This might be due either to few larvae maturing in the dung relative to the number of adult visitors, or to some larvae being missed because they matured after the pat had been sampled. Evidence that the number of *scutellaris* larvae is low relative to the number of adult visitors is given by comparison of the number of flies bred with the number of flies found on the dung. The number of *L. scutellaris* bred was strikingly low relative to the numbers found,

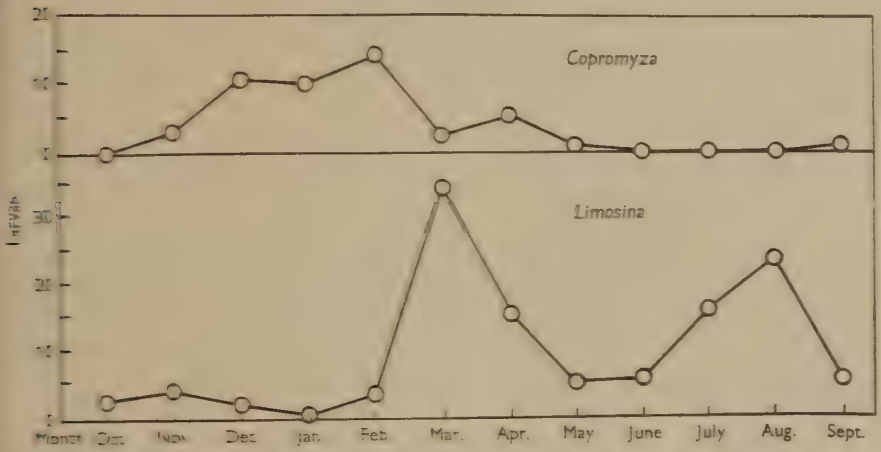

Fig. 1. The seasonal succession of larvae in cow pats. The number of larvae is recorded for each month as the geometric mean number $(n+1)$ per pat sample of four 1 in. cores of dung.

although the numbers of the other species compare favourably. Almost certainly *L. scutellaris* breeds more abundantly in another habitat. However, the numbers given previously are from pats lying in the open field. In summer, some pats are deposited whilst the cattle are sheltering from the sun during the day. These pats lie in the almost continuous shade and remain moist for a longer period. *L. scutellaris* adults in the summer are restricted to moist dung (Fig. 2) and therefore disappear from the rapidly ageing pat in the open field. In contrast to *L. lugubris*, which is abundant in the open field at this time of the year but which has not been bred from the shaded pats, *L. scutellaris* has been bred from the continuously shaded dung (fifteen adults from shaded pats compared with seven adults from pats in the open, in pats deposited on the same days in summer). The differences in preference for a different part of the field inhabited by the cattle may account for relatively few adults of *scutellaris* being bred from dung exposed in the field.

Four other species of *Limosina*, *L. spinipennis*, *L. denticulata*, *L. pusilla* and *L. aterrima*, have also been bred from cow pats (Table 5), but adults have been encountered in the field only rarely (Table 7). It is probable that these species breed more abundantly in different kinds of dung (Hafez 1949). *L. pusilla* is associated more commonly with horse dung at Rothamsted, and it is interesting to note that when horses were kept with

cattle in the same field in July 1950 this species was much more frequently found on cow pats. Hammer (1941) also records *L. pusilla* as being particularly abundant on horse dung. In Egypt *L. ferruginata* breeds mostly in horse and camel dung and rarely in cow or buffalo dung (Hafez 1949). Certainly a number of the casual species visiting cow dung (Table 2) were attracted by the moisture and not for purposes of oviposition. These species are so rare that competition with other members of the community must be very small. In a purely statistical study, however, they would be included in a species list of the habitat without reference to their rarity or to their absence as larvae feeding on the pat material (Elton 1946, Williams 1947).

Table 7. *Monthly numbers of adults of rarer species of* Limosina *in 1951*

	Feb.	Apr.	May	June	July	Aug.	Sept.
L. spinipennis	1	3	2	2	5	1	4
L. aterrima	—	—	1	2	1	—	1
L. denticulata	—	1	—	—	2	—	—
L. pusilla	—	1	—	—	2	3	2

Although three species of *Sphaerocera* were found visiting cow pats, one species being found frequently (Table 1), the genus has been bred only rarely. This emphasizes the point that the presence of adult visitors does not mean the presence of larvae living in the pat. In about 2500 sphaerocerids bred from unshaded cow pats only one male, *S. subsultans*, and one female, *S. pallidiventris*, emerged (Table 5). Probably the genus breeds more readily in manure (Thomsen & Hammer 1936).

DISCUSSION

Thirty-five species of the family Sphaeroceridae have been found associated with the cow pat community as adult flies. Of these species twenty-one are believed to be casual migrants from other habitats, as the larval stages do not live in the cow pat, and the adults probably are attracted by the moisture of the dung. A further five species are able to mature as larvae living in the pat but both larvae and adults are rare in the cow pat community at Rothamsted. Nine species have been found commonly living in the cow pat as larvae and these species are the most frequent visitors as adults.

Although an apparently simple habitat, the cow pat offers a series of niches which the species have exploited. The availability of the pat as a habitat for the larvae of any species appears to depend on the period of the year in which the adult flies can tolerate conditions in the open field. Different species utilize the pat at different times of the year. The cow pat in the winter is a different habitat for the larvae compared with the cow pat in the summer. The cattle in the winter feed mainly on hay and roots in feeding troughs set in the field. The dung deposited is coarser due to the inclusion of a large amount of straw and is less fluid than dung deposited when the cattle are grazing. The difference in texture, however, does not prevent larvae of *L. crassimana* from living in both types of dung. The difference in seasonal occurrence must be related mainly to the differences in behaviour of the adult flies in the different conditions of temperature and humidity obtained in the field at different times of the year.

During the summer pats deposited in the shade contain a different population compared with pats deposited in the open in full sunshine. *L. scutellaris* adults are attracted by moist dung and in summer this species has been bred from shaded pats, which retain their moisture longer and do not form a distinct crust so soon, whereas *L. lugubris*, a species which occurs abundantly in pats in full sunlight, has not. Several Diptera, *Scatophaga*, *Psychoda phalaenoides* L., *Copromyza hirtipes*, *Haematobia* (Laurence 1954), which live in cow dung in the larval stage, have a bimodal curve of seasonal abundance similar to that of *L. scutellaris*, occurring in spring and autumn and disappearing from the field dung in the open in summer (Hammer 1941). Larvae of these species may be found in shaded pats in the summer although rare in pats in the open.

Mohr (1943) has used the term microseral stage in describing the ageing succession of inhabitants in cow pats. Fuller (1934) has used the terms primary and secondary flies in describing the ecological succession of inhabitants of the rapidly evolving carrion community. Among those species of Sphaeroceridae which occur regularly in the summer, one group, containing *Limosina lugubris*, *L. scutellaris* and *Copromyza hirtipes*, is associated with the community of animals which develops first in the dung in the summer, and another group, containing *L. collini* and *L. pseudoleucoptera*, is associated with the community which develops later after most of the primary inhabitants have left. A similar situation is found in the genera *Sepsis* and *Psychoda* which contain a number of species inhabiting cow pats. Larvae of *Sepsis cynipsea* L. and *Psychoda phalaenoides* L. develop quickly in fresh dung whereas larvae of *Sepsis flavimana* Mg., *S. pilipes* v.d. Wulp, *Psychoda setigera* Tonn. and *P. severini* Tonn. develop later after the primary larvae have pupated (Laurence 1954). Handschin (1932) noticed that the odour and colour of field dung changed as the pat aged and suggested this as a suitable subject for a biochemical investigation. These changes in the dung may well be associated with a succession of fungi and bacteria (Pringsheim & Robinow 1947) on which the dipterous larvae may feed (Baumberger 1919).

In the family Sphaeroceridae the larvae living in the pat differ mainly in size and in the shape of the anterior and posterior spiracles (Fig. 1). There is no distinctive modification of body form as is found in the genus *Psychoda*, where the larva of *P. brevicornis* Tonn. is markedly flattened, and is said by Satchell (1947) to live on the surface of fluid dung in contrast to other larvae of *Psychoda* which feed below the surface.

Recent studies by Lack (1947) and Hartley (1953) on ecological separation of bird species have emphasized differences in feeding habits. Insects may be much more susceptible to seasonal conditions, and differences in the times of appearance of the adults in the same habitat (cyclic isolation) may be important in reducing competition between related species (Allee, Emerson, Park, Park & Schmidt 1949).

ACKNOWLEDGEMENTS

I wish to thank Dr C. B. Williams for some helpful discussion. Mr J. E. Collin and Dr O. W. Richards have determined or confirmed the determinations of a number of species of *Limosina*.

SUMMARY

1. Adults of thirty-five species of sphaerocerid flies have been found visiting cow pats lying naturally on the field at Rothamsted, Herts.

2. Fourteen of these species, of which only nine occur regularly, are shown to live in the dung in the larval stage. The other species are believed to be only casual visitors from other habitats.

3. Some of the species are shown to occupy the pat at different times of the year, although adults are recorded from a wider range of habitats in most months of the year.

4. Some of the species occupy the fresh pat whereas others have been found more commonly in the adult and larval stages associated with the pat some days old.

5. In some species the sexes possess different habits. It is suggested that the males of these species are more sensitive to low humidities than are the females.

6. The larvae of the different species differ mainly in the shape of the anterior and posterior spiracles, and some of these are figured.

7. The species of the Sphaeroceridae associated with the pat differ in their behaviour and appear to occupy different ecological niches.

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REVIEWS

THEORETICAL POPULATION DYNAMICS

Umberto D'Ancona (1954). *The Struggle for Existence.* Pp. xi + 274; 64 text-figures. Translated by Anne Charles and R. F. J. Withers. Leiden: E. J. Brill. (No price given).

This book by the well-known Italian marine biologist is primarily a systematic account of the extensive body of biomathematical theory developed by the late Vito Volterra. D'Ancona had collected data suggesting fluctuations in the populations of predatory fishes and in the abundance of other fishes forming their prey, and asked Volterra to study the problem mathematically. This Volterra did, but on an abstract level, assuming a very simplified picture; becoming engrossed in this study, he devoted himself to the building of a novel and imposing edifice of abstract reasoning. Studies of what he considered to be the essential relationships of competing species, and of predators and their prey, were developed mathematically in a series of papers published in the 1920's and 1930's. A good deal of it has not been available in English before.

D'Ancona has added summary accounts of a considerable amount of similar work by other authors, and has provided a few introductory and concluding chapters in an attempt to bring the theoretical work into relation with practical ecology and to present the subject in perspective. The book covers much of the same ground as Kostitzin's *Mathematical Biology*, but more comprehensively and in more detail. The first edition was published in German in 1939, and a second in Italian; the present volume is a translation of a new and revised Italian edition.

There is a bibliography of some 350 references, in which the work of the past decade is covered rather patchily compared with the pre-war literature. It could have been greatly improved by the insertion of page numbers to show where the references are quoted in the text, particularly since there is no index. The format is satisfactory, but there are certain errors and misprints, some of them confusing, e.g. 'causal' instead of 'casual' on p. 189, 'fish' instead of 'fishing' on p. 209, 'date' instead of 'data' on p. 274, 'flour' instead of 'grain' on p. 232. A few references in the text are omitted from the bibliography.

The first four chapters give an elementary account of the ecological ideas involved in population dynamics. Chapter 5 deals briefly with the attempts of Farr, Brownlee, Lotka and others to make mathematical models of the population relationships in the field of epidemiology. The aim of this work was to deduce, from simplified but otherwise reasonable assumptions, conclusions which matched the observed facts, or which would suggest undetected relationships. How successful were these efforts? Observations said to bear out some of the theoretical conclusions are referred to with disappointing brevity and vagueness. The chapter concludes with a similarly brief account of some equations formulated by W. R. Thompson (1922 and later) in a theoretical study of the reduction of hosts by insect parasites.

Chapter 6 deals with aspects of a more general mathematical study of biological 'equilibria', undertaken by Lotka (1925). He was apparently the first to make the important deduction that interspecific relationships, such as those between populations of insects and their parasites, could give rise to cyclic fluctuations of both species.

Chapter 7 introduces Volterra's work, 'a mathematical theory of the struggle for existence', which is claimed to be 'a complete theory of interspecific relations'. To avoid making the mathematics impossibly complicated, Volterra begins with 'very simple ideal associations, taking no account of accessory factors. Subsequently, he gradually complicates the primitive hypotheses, successively considering other factors and circumstances, thus always coming nearer to the conditions which occur in associations in nature.'

In the main section of the book, chapters 8–24 (122 pages) Volterra's work is presented systematically, step by step (but frequently without references!), the mathematical passages being strung together with textual explanations, summaries and conclusions. The mathematics are chiefly in the form of differential equations. Work of the same type by other authors is brought in where it bears on the topic under discussion. The succession of topics begins with the increase of an isolated species and encounters of the sexes, going on to associations of two

species competing for food, or one eating the other, associations of more than two species, taking in a consideration of the stationary state (when there is no sustained increase or decrease), of fluctuations, and of disturbances caused by immigration, to make no mention of a number of items labelled with specially coined terms and difficult to explain briefly. At an early stage we come upon Volterra's now well-known laws of associations of predator and prey (the Law of Periodic Cycle, the Law of the Conservation of Averages, and the Law of the Disturbance of the Averages).

In Chapter 25, the author leaves Volterra's work to give a brief general account of the analogous mathematical studies of Hardy, Fisher, Haldane, Sewall-Wright and others on the struggle for existence in relation to evolution. The work of Nicholson and Bailey, whose methods and assumptions differ from Volterra's, is dealt with in a few sentences in a chapter on 'Other Extensions of Volterra's Theory'.

The last four chapters deal with questions of the greatest interest to biologists who are wondering how seriously mathematical theorizing like Volterra's deserves to be taken. It is a pity that crucial passages are weakened by overstatements and a rather casual treatment of the evidence. Chapter 27 is headed, 'Some Remarks of Justification and Evaluation of the Application of Mathematics to the Study of Associations'. Volterra's theory, it is admitted, has been elaborated purely theoretically. 'This development of the mathematical theory of biocoenoses may seem unsatisfactory to the naturalist accustomed to give importance to that which is the fruit of observation and experiment. In fact, we might say that the majority of naturalists, accustomed to studying nature empirically, are, by reason of their own habits of mind, loth to accept the fruits of pure speculation, or anything which does not derive directly from observation and experiments but starts from theoretical premisses. Such diffidence is, however, unjustified.' Volterra, we are told, is only repeating what has been done in the physical sciences. Biology uses the same methodology: 'The development which the biological sciences have undergone in recent times can be said to be exclusively the fruit of the application to them of the methods of physics and chemistry.'

This is nonsense. It is true that ecology uses the same scientific method as physics, and that ecologists need to study physical conditions as well as biological relationships; but ecology has its own problems on its own level, and the inter-relationships of animals are analogous only in a very general way to physical phenomena. Moreover, it is grossly misleading to say that theory has generally preceded practice, especially in mechanics, as claimed in several places in the book. Theory has sometimes leaped ahead of practical observation and experiment, and often lagged behind; progress is surest when they keep in touch with each other. Sometimes when theory has gone far ahead, it has taken a wrong path, and a great deal of effort has been misdirected. There is no certainty for theorists, and it is always necessary to examine whether or not a particular theory is soundly based, and to find out whether or not it is vindicated by observation and experiment. It is the latter question one hopes to find answered in the concluding chapters in defence of Volterra's theory.

The author goes on to point out some of the advantages of mathematical theory, in forcing us to make our postulates clear and precise, showing us clearly what are the consequences of these assumptions, and suggesting new hypotheses. But again we are presented with some misleading statements, such as that in mathematical physics 'one does not start out from a mathematical analysis of experimental facts, but elaborates a mathematical theory whose confirmation is then sought in experimental verification'. This opening phrase ignores the existence of the relatively vast body of well-established practical data which the physical theorist has to stand upon, in contrast to the flimsy and tentative perch of the ecologist. Nevertheless, we can agree when D'Ancona writes that 'If the application of formulae and theorems to the experimental treatment of associations is still difficult, the study of associations can be motivated, developed and directed by this theoretical research, which allows us to see possible links which would not be demonstrated by empirical examination alone.' It can be, subject to a wise (or lucky) choice of theory.

Chapter 28 deals with 'Empirical Evidence for Volterra's Theory'. Here D'Ancona presents his own data from Italian fish markets, and claims that the relative numbers of predatory Selachians increased in the war periods when fishing was suspended. This conclusion is brought in support of Volterra's Law of the Disturbance of Averages, which predicts that when predators and prey are eliminated in equal proportion, the prey will increase and the predators decrease. D'Ancona's interpretation has been challenged, and the graphs he presents are not convincing

without tests of significance. The author makes briefer references to Elton's data on population cycles, also to Middleton, Errington, and others, and considers these cycles 'are the result of complex interferences of environmental, physical and biological factors of cohabitation'. Some further supposed examples of correspondence with the theory are mentioned and some criticisms by Bailey and Sewertzoff are discussed, but all too briefly to be satisfying. What has promised to be a crucial chapter is finally disappointing, because of the vague and indecisive way in which the observed cases are compared with the requirements of the theory. But perhaps this is more a reflexion on the state of ecological knowledge than a reproach to the author.

D'Ancona is in a happier position in Chapter 29, on 'Experimental Confirmation of Volterra's Theory', for there are the well-known experiments of Gause with interacting micro-organisms and with mites, set out in fair detail to exemplify predator-prey cycles and other aspects of the theory. Crombie's experiments on crowding effects and competition in populations of storage pest insects are also given due prominence. Crombie (1945) discussed the relevance and implications of one of Volterra's basic equations for the processes of competition in these insects. There is a briefer account of the work on *Tribolium*, of MacLagan's experiments on density effects in *Tribolium* and *Calandra*, and of other work on insects and on micro-organisms, presented in a somewhat inconsequential way; all sorts of interaction effects seem to be 'confirmations of Volterra'. One feels the author has missed opportunities here of making a more searching analysis of some of this work, and bringing out more clearly the points of agreement and disagreement with the theoretical conclusions. A carefully designed laboratory experiment can bring the mathematics to life; if the theory cannot be demonstrated in this way, there is little hope for it amidst the complicated cross-currents of field ecology.

The final chapter discusses the ecology of food-production, particularly the conditions for maximum productivity in fisheries. The author expresses the belief that great progress can be made in such fields along the lines of Volterra's theory. This is very likely true, provided that such theory is newly developed on a solid basis of ascertained fact. Volterra's theory itself has too abstract a basis to be relied upon as a guide in such work, or indeed in most other ecological investigations. Nevertheless, it has thrown up some ideas that have had great influence, notably the 'Law' of predator-prey oscillations; and it has certainly demonstrated that biomathematical theory is potentially a subject of major importance for ecology—probably more important than we can easily realize at present. Volterra's work must be assessed as a pioneering achievement. D'Ancona's book marks a step forward in the integration of a new subject within ecology, and provides a comprehensive account of Volterra's special contribution to it.

M. E. SOLOMON

THE BIOLOGY OF SQUIRRELS

Monica Shorten (1954). *Squirrels.* Pp. 212, illustrated. London: Collins. (New Naturalist Monograph 12.) Price 15*s*.

In this excellent monograph the author brings together everything that is known of the history and biology of *Sciurus vulgaris* and *S. carolinensis* in Britain; she is well qualified to do so for she has been carrying out research on these animals for over ten years, during which she has written several papers about them, some of which have appeared in this *Journal*.

The fluctuations in the numbers of animal populations have received much attention from zoologists in recent years, so that the decline of the red squirrel and the rise of the grey since its introduction are matters of great scientific interest, apart from their economic importance. Unfortunately no censuses of population have been carried out, and although the broad story is known, no figures are available for statistical analysis. The author's sample censuses when supplemented by further work will doubtless supply much valuable information, and in the meantime the only figures we have are numbers of grey squirrels killed annually in each county—in 1952 the total kill for the year recorded in England and Wales was 168 038, a total that has since been considerably exceeded owing to the bonus scheme of payment for tails.

It is usually agreed that the ancestral home of the red squirrel was dense secluded coniferous woodland, but when the species became very abundant at the beginning of the present century it could be found in most of the types of habitat now used by the grey. Although there is a widespread belief that the grey squirrel is responsible for the present scarcity of the native

red squirrel, the author shows that the latter has decreased through epidemic disease and man's destruction of its woodland habitat; in addition red squirrels were so abundant and destructive no more than forty years ago that squirrel clubs and 'warfare of extermination' were organized against them. The grey squirrel seems to be an opportunist that has grabbed the ecological niche left vacant by the decline in numbers of the red. It is ironic that in Britain legislation directs the destruction of the grey squirrel as an unmitigated pest, but in America it conserves the species for 'hunting' during a restricted open season. 'Much of the grey's unpopularity is due to the fact that it has too high a population for our comfort; the red is but a charming memory from childhood days, and is forgiven all. Yet each crime for which the grey is now blamed was paralleled in the days (only fifty years ago) when the red was superabundant.... Neither squirrel would be a menace to man if present in small numbers.'

In addition to the detailed history of both species of squirrel in Britain, and a close analysis of the spread of the alien species during the present century, this book contains valuable chapters on the breeding and development of the grey squirrel—and of the red too, as far as it is known—the pelage and its seasonal changes, the relationship between the two species, their destructiveness to human interests, and measures of control. It even contains a number of recipes for cooking squirrels, which are excellent 'table birds'.

Monica Shorten has made a very real contribution to biology, and in particular to ecology, in her studies of the grey and red squirrels; this volume very appropriately brings together the results of her own researches with all those recorded in the literature. It is a pity that the text is marred by a number of misprints—and the travesty on the jacket is hopelessly out of drawing, as can be verified by a glance at the photograph reproduced on Plate 12.

L. HARRISON MATTHEWS

A MONOGRAPH ON THE HERON

Frank A. Lowe (1954). *The Heron.* Pp. xiii + 177; 1 coloured and 8 black-and-white plates; 12 text-figures. London: Collins. (New Naturalist Series.) Price 18*s*.

The heron is a bird which a great many people must know by sight, because of its large size and unusual form, so that this monograph should appeal to a wide public. Frank Lowe has spent over twenty years studying the heron in the field and in particular he has concentrated on one colony in Dam Wood, between Southport and Ormskirk in Lancashire. He has also studied the literature extensively and there is a bibliography of eleven pages, but there are few references to this in the text by means of dates after authors' names, which seems a mistake in a monograph of this nature.

After a description of the physical features and specializations of the heron, there are chapters on world distribution and the population of Britain. *Ardea cinerea* has an astonishing range extending over most of the continents of Europe, Asia and Africa; its breeding range and winter distribution, and those of the American *A. herodias*, are shown on two map projections of the world, with the zones of the subspecies. The heron is a most convenient bird for census work and we now have a fair idea of the British population and its changes over the last twenty-seven years, which are conveniently summarized and discussed here. In the chapter on food and foraging the heron is shown to have catholic tastes which enable it to survive over a wide terrain. The commonest prey are fish, frogs, beetles, moles, water-voles and rats, but vegetable matter is also eaten, probably for pellet formation. Remains of fish are not found in the pellets, since their bones are reduced to a liquid state by the digestive juices, but it is mainly as a fish-eater that the bird is known by fishermen, who are apt to regard it as vermin. Observation shows, however, that the heron normally takes only small trout and that it has a marked preference for eels, which are important enemies of trout and salmon, and the author considers that on balance it may even be beneficial to fisheries.

Frank Lowe has spent over 400 hours in tree-top hides at his heronry, and the detailed descriptions of the breeding biology are based on his observations from these: dance gathering, nest occupation, display, incubation and development of the young. Young herons remain in the nest for eight weeks and after a further two weeks they begin dispersing. The extensive ringing returns from Britain and continental Europe are analysed and the journeys plotted on three useful maps to show the movements of herons to and from Britain, and heron migrations over Europe as a whole. In Britain with its more equable climate there is no marked directional

trend in the dispersal movements, but on the continent movements do become directional and towards the south, so that Scandinavian herons visit Britain and north German birds may travel as far as Africa. Two final chapters describe the heron in history and folklore, and the hunting and eating of herons.

The book is illustrated with one coloured plate and a number of fine black-and-white photographs, mostly by Eric Hosking and the author, but it is a pity that the reader is not referred to any of these in the text. The description of display, for example, could have been made clearer by references to the photographs showing different types, especially as the first two of these are separated from the description by over fifty pages. The chronological account of the development of the young birds would also have become more vivid with references to the photographs, on which there is no indication of the age of the young. These however are minor criticisms and the book is a valuable contribution to bird literature, both for the original work described in it and for the collection and synthesis of much information.

P. F. HOLMES

A GUIDE TO CANADIAN FISH

W. B. Scott (1954). *Freshwater Fishes of Eastern Canada.* Pp. xiv + 128, 2 text-figures, 108 photographs (by W. H. Carrick), 1 map. Toronto: University of Toronto Press; London: Geoffrey Cumberlege. (No price given).

This book sets out to provide a handy guide for anglers, commercial fishermen and naturalists to the 142 known species of freshwater fish in Eastern Canada (Ontario, Quebec, Newfoundland and the Maritime Provinces). Most of the book consists of a species by species 'array'. Usually a page is devoted to each species, with a monochrome photograph, the scientific name, common names, and short paragraphs on distinguishing features, size, occurrence, life history and habits, and comments on value for commercial and sport fishing, edibility, etc.

The primary use of the book will be taxonomic, and on the whole the photographs and descriptions are adequate for this purpose. No attempt is made to provide any keys, or the means to distinguish accurately a number of the rare or difficult species. This is probably justified, for such identifications would be beyond the ability of the laymen for whom the book is intended. Nevertheless, some important species that are frequently confused (e.g. *Salmo trutta* and *S. salar*) might have been given longer treatment and the aid of line diagrams to show key characters. As far as it goes the other information given is good and to the point. Ecological notes include the food eaten, habitats and spawning habits, and the importance of the species as food for other fish as well as man.

Dr W. J. K. Harkness contributes, as a foreword, a really excellent six page essay on the management of freshwater fisheries. There is a brief introduction, a short list of references and a good index, but the cover and binding would not last long in the knapsack of a back-woods angler. Biologists in the region when identifying fish will probably still use one of the other books such as Hubbs and Lagler's *Fishes of the Great Lakes* (1947), but Scott's book deserves to have a wide use among fishermen and amateurs.

E. D. LE CREN

SHORE INVERTEBRATES

S. F. Light, revised by **R. I. Smith, F. A. Pitelka, D. P. Abbot, and F. M. Weesner (1954).** *Intertidal Invertebrates of the Central California Coast.* Pp. xiv + 446; 138 text-figures. Berkeley: University of California Press; London: Cambridge University Press. Price 37*s.* 6*d.*

The late Professor S. F. Light, who died prematurely at the age of 61, was a member of the staff of the Zoology Department of the University of California at Berkeley, for twenty-two years. During that time he produced a manual for the use of students of the marine invertebrates of the Californian coast, entitled *Laboratory and Field Text in Invertebrate Zoology*. At the time of his death the first edition of this work was practically out of print, and the author had only carried out a small part of the revision required for a new edition. After his death this revision was continued by Dr Ralph Smith and his collaborators in the tradition of the first edition; but the revisers have done a good deal of re-writing, and have aimed at widening the

appeal of the text so that it will now be useful beyond the rather narrow limits within which it was originally conceived. The area covered by the book is (approximately) the Californian coast between Carmel and Bodega Bay, and its object is to provide not only a general introduction to the marine invertebrates, but also keys and illustrations which will enable students to identify the commoner animals belonging to the various groups and inhabiting this area. The bulk of the text consists of these items, and they appear to be very well compiled. Certainly there can be few marine areas for which a recent guide as detailed and comprehensive as this is available, and the editors, as well as Dr Light, are much to be congratulated on it. There is a short section on marine algae and flowering plants, and a longer one entitled 'Field studies'. This ensures that the students will not have their attention directed exclusively to the taxonomic aspect of the subject, and after a general introduction on food, reproduction and environmental conditions, it presents a number of 'field exercises' which can be carried out with profit at various named points or in specific habitats on the coast, or which present particular ecological problems for solution. The book is completed by a considerable bibliography. It will be used with greatest benefit in conjunction with other books covering the field in a different way, such as Ricketts and Calvin's *Between Pacific Tides*.

T. A. STEPHENSON

TAXONOMIC KEYS

K. H. Mann (1954). *A Key to the British Freshwater Leeches with notes on their Ecology*. Pp. 21; 1 coloured plate, 41 text-figures. Freshwater Biological Association Scientific Publication No. 14. Price 2*s*. 6*d*.

For some years there has been a need for a modern key to the British leeches in some accessible publication, and in this work Dr K. H. Mann has supplied exactly what was wanted. In an introduction he gives first an up-to-date list of species side by side with a list of the old names which most people have used since Harding's monograph of 1910. The list includes two species which the author has recently recorded for the first time in Britain, and he expresses the hope that the use of the key may extend the known range of these. *Protoclepsis*, *Glossosiphonia* and *Herpobdella* have become *Theromyzon*, *Glossiphonia* and *Erpobdella*, and it is important to note the change in the species of *Erpobdella*, since *atomaria* of Harding is now *octoculata* and *octoculata* of Harding is now *testacea*. There is a useful section on the techniques of narcotizing and preserving leeches, and of removing the genital atria. The key itself, which is illustrated with 38 text-figures, seems admirably clear. Particularly welcome are the figures showing the distinction between the genital atria of the two *Erpobdella* species and the exact position and variation of the eyes in the species of *Glossiphonia*, though some account of the colouring of the latter might well have been included. In some notes on the ecology of leeches after the key, the author describes the feeding habits and distribution of each species, mainly from his studies in the Lake District (soft water) and Berkshire (hard water).

A very successful innovation for this series of publications is the inclusion of a full-page coloured plate, reproduced from a painting by Dr E. V. Watson. This shows the appearance in dorsal view of all the truly aquatic species, except the two rare ones recorded recently, and it makes the publication extremely good value at 2*s*. 6*d*.

P. F. HOLMES

D. E. Kimmins (1954). *A Revised Key to the Adults of the British Species of Ephemeroptera*. Pp. 71; 30 text-figures. Freshwater Biological Association, Scientific Publication No. 15. Price 3*s*.

No biologist, or angler, with an interest in the fauna of streams will be unfamiliar with the first edition of this key. The revised work exhibits, and even improves upon, those features which mark the original as one of those rare publications—a key that really works; moreover, one which is easily followed even by the beginner, and which has ample text-figures to illustrate each feature as it arises.

The one major alteration, the elimination of the key to the families of genera and nymphs, is a disappointing one. It is explained that there will be a complete key in a later number of

the series; meanwhile however, since the first edition is out of print, there will be for newcomers no way of identifying the nymphs except by pursuing the rather scattered literature. It is always a matter for regret when keys to adults and nymphs cannot be published in the one volume, and especially is this so for a small group like the mayflies. The Scientific Publications of the F.B.A. must often be used by students, who too often draw a distinct line between water and land collecting (how many field trips include both?); it would seem a pity to emphasize the dichotomy.

J. E. HARKER

BOOKS RECEIVED

Genetic Homeostasis. By I. MICHAEL LERNER. Edinburgh and London: Oliver and Boyd. 1954. Price 12*s*. 6*d*.

Biology of Deserts: the Proceedings of a Symposium on the Biology of Hot and Cold Deserts organized by the Institute of Biology. Edited by J. L. CLOUDSLEY-THOMPSON. London: Institute of Biology. 1954. (No price given.)

The Natural Regulation of Animal Numbers. By DAVID LACK. Oxford: Clarendon Press. 1954. Price 35*s*.

Ninth Report of the Biological Bureau. Quebec: Province of Quebec, Game and Fisheries Department. 1953. (No price given.)

Malayan Animal Life. By M. W. F. TWEEDIE and J. L. HARRISON. London: Longmans. 1954. Price 18*s*.

Pine looper moth (Bupalus piniarius). Forestry Commission leaflet No. 32. London: H.M.S.O. 1954. Price 9*d*.

ABSTRACTS

The abstracts are edited by Prof. L. A. Harvey with the assistance in selection and abstracting of J. D. Brayshaw, D. H. Chitty, G. I. Crawford, T. A. W. Davis, A. E. Ellis, P. D. Gabbutt, Miss U. Grigg, N. A. Holme, S. J. Holt, D. Leatherdale, A. Macfadyen, C. Matheson, Miss E. Nelmes, G. G. Vickers, Mrs M. Vincent and M. Williamson. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations can greatly aid this work by making sure that copies of their publications are sent regularly to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford**. It has recently become noticeable that some organizations have sent their material only at irregular intervals. Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Prof. L. A. Harvey, University College, Exeter**. Thanks to the help volunteered by new abstractors, whose names are listed above, a much more complete cover of journals and publications is now possible. Nevertheless, the services of one or two more helpers will be welcome in order that we may provide a synopsis of all publications likely to be of interest to British ecologists.

Separate copies of the abstracts can be obtained from **The Cambridge University Press, 200 Euston Road, London, N.W. 1,** or through any bookseller; price 5*s.* 6*d.* per annum, post free (issued in May and November). Back numbers of the 'Notices of publications...' from Vol. 3 (1934) to Vol. 20 (1951) may also be held at 2*s.* for each annual set of two parts.

CONTENTS

Note. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:
(*a*) papers in *Bird Notes* and *British Birds* which would fall in '4. Food and food habits';
(*b*) papers in the above two journals and in *The Entomologist's Record* and *The Entomologist's Monthly Magazine* which would be classified in '5. Migration, introductions and local distribution'.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and Brackish

Bagenal, T. B. (1954). The growth rate of the hake, *Merluccius merluccius* (L.), in the Clyde and other Scottish sea areas. *J. Mar. Biol. Ass. U.K.* **33**, 69–95.

Growth rate in the Clyde was studied from size-frequency distribution of the catches, and by examination of otoliths. A comparison is made with growth rates in other areas.

Bainbridge, R. (1953). Studies on the interrelationships of zooplankton and phytoplankton. *J. Mar. Biol. Ass. U.K.* **32**, 385–447.

An apparatus in which it is possible to observe the horizontal migration of zooplankton in concentration gradients of phytoplankton is described. Results of experiments on the behaviour of certain animals in gradients of diatoms and flagellates are given. A second apparatus for observing vertical migrations is also described, and an account given of the results obtained. The possible application of these observations towards resolving the problem of the inverse distribution of phyto- and zooplankton in the sea is discussed.

Bowers, A. B. (1954). Breeding and growth of whiting (*Gadus merlangus* L.) in Isle of Man waters. *J. Mar. Biol. Ass. U.K.* **33**, 97–122.

Seasonal changes in the gonad, and age and growth, are described. Age determinations were made from otoliths, in which a translucent band is laid down annually.

Chipperfield, P. N. J. (1953). Observations on the breeding and settlement of *Mytilus edulis* (L.) in British waters. *J. Mar. Biol. Ass. U.K.* **32**, 449–476.

The season of development of gonads and spawning from a number of localities are compared. Conditions which may induce spawning are discussed. Information is given on the density of spat settlement at different levels in the littoral zone.

Crisp, D. J. (1954). The breeding of *Balanus porcatus* (da Costa) in the Irish Sea. *J. Mar. Biol. Ass. U.K.* **33**, 473–496.

An account of breeding, length of larval life, and development of sexual organs in this cross-fertilizing hermaphrodite barnacle. Data on rates of shell growth and longevity are given.

Cushing, D. H. (1953). Studies on plankton populations. *J. Cons. Int. Explor. Mer*, **19**, 3–22.

Growth and distribution of dense patches of zooplankton, and relation to distribution of herring.

Evans, G. O. & Browning, E. (1953). Some inter-tidal mites from south-west England. *Bull. Brit. Mus. Nat. Hist. Zool.* **1**, 413–422.

Notes distribution of ten species of inter-tidal Acari in south-west England, with brief habitat notes and descriptions. Describes *Lasioseius fucicola* Halbert 1920, and *Chausseria maritima* sp.n.

Glynne-Williams, J. & Hobart, J. (1952). Studies on the crevice fauna of a selected shore in Anglesey. *Proc. Zool. Soc. Lond.* **122**, 797–824.

Physical measurements of microclimate and tidal levels are related to the fauna of 49 species; these include a terrestrial and a marine element. There is strict limitation as to vertical level and terrestrial forms are more usual deeper in the crevices. Feeding studies in field and laboratory are used to construct a 'food-web' and the presence of two alternating 'food chains' corresponding to the two faunal elements is demonstrated.

Holme, N. A. (1954). The ecology of British species of *Ensis*. *J. Mar. Biol. Ass. U.K.* **33**, 145–172.

Factors believed to be concerned in the distribution of three species of *Ensis* are described. Soil grade and wave exposure appear to be the most important limiting factors.

Knight-Jones, E. W. (1953). Decreased discrimination during setting after prolonged planktonic life in larvae of *Spirorbis borealis* (Serpulidae). *J. Mar. Biol. Ass. U.K.* **32**, 337–345.

Freshly liberated *Spirorbis* larvae settle more readily on surfaces bearing previously settled individuals than on bare controls, but larvae kept swimming for three hours or longer exercise less choice when settling. When larvae are freshly liberated there is a great difference between the rates of settling gregariously and in isolation, but after they have been kept swimming for three hours this difference becomes less marked.

Millar, R. H. (1954). The annual growth and reproductive cycle of the ascidian *Dendrodoa grossularia* (van Beneden). *J. Mar. Biol. Ass. U.K.* **33**, 33–48.

An account of growth, development of the gonad and breeding in populations from Essex and the Firth of Clyde.

Morton, J. E. (1954). The crevice faunas of the upper intertidal zone at Wembury. *J. Mar. Biol. Ass. U.K.* **33**, 187–224.

An account of the quantitative distribution of species inhabiting rock crevices on the shore. Ecological factors which may affect distribution within the crevices are discussed. The probable course of succession resulting from the weathering of the substratum and deepening of the crevice is described.

Nédélec, C. (1954). Données Biométriques sur le Thon Rouge de la Mer du Nord. *J. Cons. Int. Explor. Mer*, **19**, 350–355.

Racial study. Comparison with Mediterranean population.

Nielsen, E. Steemann (1954). On organic production in the oceans. *J. Cons. Int. Explor. Mer*, **19**, 309–328.

Estimation of phytoplankton production from the rate of assimilation of radio-active carbon.

Rees, W. J. & Lumby, J. R. (1954). The abundance of *Octopus* in the English Channel. *J. Mar. Biol. Ass. U.K.* **33**, 515–536.

A consideration of causes of the 'plague' of octopus on the English channel coast in 1950–51. Planktonic larvae originate mainly from breeding centres on the French coast, there being no indication of substantial breeding on the English coast. The distribution of octopus seems to be little influenced by sea temperature, but a dearth of food may be the cause of a subsequent trans-Channel migration of adults.

Rendall, R. (1954). A survey of some Orkney beaches. *J. Conchol.* **23**, 390–394.

Habitats of marine Mollusca on islands of Stronsay and North Ronaldsay.

Russell, F. S. (1953). The English Channel. *Rep. Devon. Ass. Adv. Sci.* **85**, 1–17.

A summary review of the hydrographical and biological conditions in the English Channel, with a discussion of the phenomena underlying fluctuations in the characters of the waters and of the flora and fauna.

Simpson, A. C. (1953). Some observations on the mortality of fish and the distribution of plankton in the Southern North Sea during the cold winter, 1946–1947. *J. Cons. Int. Explor. Mer*, **19**, 150–177.

Effects of unusually cold weather on fish stocks.

Southward, A. J. & Orton, J. H. (1954). The effects of wave-action on the distribution and numbers of the commoner plants and animals living on the Plymouth Breakwater. *J. Mar. Biol. Ass. U.K.* **33**, 1–19.

A comparison of the fauna and flora on the exposed and sheltered sides of the breakwater. Many algae were more abundant on the sheltered side, but the majority of the animals were favoured by the greater wave-action on the exposed side.

Wilson, D. P. (1954). The attractive factor in the settlement of *Ophelia bicornis* Savigny. *J. Mar. Biol. Ass. U.K.* **33**, 361–380.

Acid-cleaned sands become more attractive to the larvae of this polychaete if treated in such a way as to encourage the growth of micro-organisms on the grains.

Wilson, D. P. & Armstrong, F. A. J. (1954). Biological differences between sea waters: experiments in 1953. *J. Mar. Biol. Ass. U.K.* **33**, 347–360.

Further experiments on the development of *Echinus* larvae in Clyde and English Channel waters, in an attempt to find the factors responsible for the more healthy development of larvae in Clyde water.

(*b*) Fresh Water

Allen, S. E. (1954). Aestivating habits of Hydradephaga (Col.). *Ent. Mon. Mag.* **90**, 91–92.

Marked adults of *Agabus bipustulatus* and *A. labiatus* in a ditch in an area where the water-level was very sensitive to weather changes tended to move under wet conditions and remain in a limited area under dry.

Brown, E. S. (1954). Notes on the rarer British species of aquatic and semi-aquatic Hemiptera: II Veliidae. *Entomologist*, **87**, 45–53.

Observations on the ecological requirements of *Microvelia pygmaea*, and the distribution of *Velia caprai* and *V. saulii*, including new county records for all three.

Corbet, P. S. (1954). Seasonal regulation in British dragonflies. *Nature, Lond.* **174**, 655.

In the life history of *Anax imperator* the synchronization of emergence (90 % of adults emerge within first ten days of emergence period) is a direct consequence of the diapause in the final larval instar. Dragonflies typified by this type of life history are termed 'spring' species. In 'summer' species the diapause, if present, is located elsewhere in the life history and growth is uninterrupted in the final larval instar. Synchronization, therefore, is not so marked in the 'summer' species. The wider implications of this ecological classification, when applied to the British species, is briefly discussed.

Grainger, J. N. R. (1952). The *Diaptomus* fauna of some lakes in S.W. Ireland. *Proc. R. Irish Acad.* **54** B, 217–224.

Surveys the distribution of four species of this copepod in lakes in south-west Ireland, particularly in the smaller mountain lakes of Co. Kerry. This is discussed in relation to the biotic conditions of the lakes and to the distribution of the species elsewhere in Britain.

Green, J. (1953). Records of Peritrichs (Protozoa, Ciliata) on aquatic insects. *Ent. Mon. Mag.* **89**, 107.

Species found on *Caenis, Cloeon dipterum, Coenagrion* sp., *Ilyocoris cimicoides, Plea leachii, Notonecta glauca, Corixa punctata, C. concinna* and *Chironomus plumosus* during February and May 1952 in London and Essex.

Hall, R. E. (1953). Observations on the hatching of eggs of *Cheirocephalus diaphanus* Prévost. *Proc. Zool. Soc. Lond.* **123**, 95–109.

The known irregular appearance of this species and its ability to breed continuously under suitable conditions are largely accounted for by observations on the breaking of egg membranes and experiments on the effects of dessication.

Hardisty, M. W. (1954). Sex ratio in spawning populations of *Lampetra planeri*. *Nature, Lond.* **173**, 874–875.

Observations made over a number of years show that the sex ratio varies in different streams and even from year to year.

Healy, A. (1953). Trout in Lough Rea, Co. Galway. *Sci. Proc. R. Dublin Soc.* (N.S.) **26**, 157–164.

The scales, weight/length ratio, and stomach contents of brown trout caught by the Lough Rea Anglers' Association from 1948 to 1953 were investigated. The growth-rate was high, a point of interest in view of the fact that some of the trout are descendants of small, slow-growing trout from Lough Atorick; the increment in growth was at a maximum in the second year. The rise in K, the condition coefficient, from May to June varied between 0·91 and 1·01 in the five years. Weight increments increased up to the fourth year and then decreased. Insect larvae, chironomid pupae and *Asellus* formed the bulk of the food.

Hunter, W. R. (1953). A note on the amphibious snail *Succinea pfeifferi* Rossmässler, in a previously undescribed habitat. *Glasg. Nat.* **17**, 91.

A microhabitat on the shores of Loch Lomond, heaps of dead leaves along the strand-line in autumn, and bundles of dead leaves in small streams flowing into the loch.

Jones, J. R. Erichsen (1953). The reactions of fish to water of low oxygen concentration. *J. Exp. Biol.* **29**, 403–415.

Experimental results for *Gasterosteus aculeatus*, *Phoxinus phoxinus* and *Salmo trutta* show that water of low oxygen tension is avoided by these species on account of a very rapid onset of respiratory distress, followed by random movements; the fish appear to have no immediate appreciation of low oxygen tension.

Jones, J. W. (1953). Salmon studies 1951. *Fish. Invest., Lond.* (1) **5**, 1–16.

Analyses of salmon scales from the Cumberland Derwent, 1951, Cheshire Dee, 1951 and 1937–51, and of salmon and sea trout scales from the Esk (N. Yorkshire), 1950, with inferential data on life histories and migrations.

Lansbury, I. (1954). Some notes on the ecology of the aquatic and semi-aquatic Hemiptera-Heteroptera and Coleoptera of four bomb-craters in Fairmead Bottom, Epping Forest, Essex. *Entomologist*, **87**, 77–82.

Contains lists, with dates, of the Hemiptera, Coleoptera and other insects, amphibia and plants in each of four flooded bomb craters, which are described, together with notes on the status of some of the Hemiptera, the habitats occupied by them in the ponds, and the mode of colonization.

Lansbury, I. (1954). Some notes on the ecology of *Corixa* (*Halicorixa*) *stagnalis* Leach, with some information on the measurement of salinity of brackish habitats. *Ent. Mon. Mag.* **90**, 139–140.

The method of measuring salinity described utilizes the relation between the density, temperature and salinity of water. *Corixa stagnalis* appears to occur in widely different habitats, though showing a preference for variable associations of sand-clays with black and yellow oozes, and is known from waters with salinities of 3·19 and 20·75 g per litre.

Schuster, W. H., Kesteven, G. L. & Collins, G. E. P. (1954). Fish farming and inland fishery management in rural economy. *FAO Fisheries Study* No. 3, 64 pp. Rome.

A general review of the subject largely from the ecological viewpoint.

Stokoe, R. (1954). Siddick Pond and its birds. *Trans. Carlisle Nat. Hist. Soc.* **8**, 33–74.

A survey of a large pond near the coast of Cumberland, based on a report prepared for the Nature Conservancy. The history of the pond, the chemical analysis of the water, and bacteriological counts are given, with notes on the invertebrate and other vertebrate animals. The main part of the paper is a systematic list of 121 birds reported from the pond over a period of thirty years, with detailed accounts of the water birds.

(*c*) LAND

Allen, D. E. & Cowin, W. S. (1954). The flora and fauna of the Isle of Man and their geographical relationships. *Northw. Nat.* (N.S.), **2**, 18–30.

The animals considered in this discussion are chiefly insects, birds and mammals.

Andrew, D. G. (1951). The building of a rookery. *Brit. Birds*, **44**, 129.

Observations on a new rookery of five pairs in Cambridge during March, 1949.

Armstrong, E. A. (1950). The behaviour and breeding biology of the Iceland Wren. *Ibis*, **92**, 384–401.

Field observations of *Troglodytes troglodytes islandicus* in the early part of the breeding season, and data obtained by previous observers. Comparisons with related subspecies are made.

Ash, J. (1951). The effect of a snow-storm on breeding birds. *Brit. Birds*, **44**, 57–59.

The effect of a severe snow-storm on 26 April 1950 at Sunninghill, Berkshire, on 37 nests of fourteen species of birds, excluding nests of hole nesters which were not affected. Small passerines were the worst sufferers; Corvidae, a *Falco tinnunculus* and a *Vanellus vanellus* did not desert.

Ash, J. (1953). Notes on the puparial stage of some Hippoboscidae (Dipt.). *Ent. Mon. Mag.* **89**, 206–207.

Data on the pupal and adult survival periods of *Crataerina pallida*, *Ornithomya avicularia* and *O. fringillina*, from which it is concluded that each produces one generation a year.

Baldwin, P. H. (1953). Annual cycle, environment and evolution in the Hawaiian honeycreepers (Aves: Drepaniidae). *Univ. Calif. Pubns. Zool.* **52**, 285–398.

A comprehensive study of an island population, which discusses the distribution, structure and evolution of the various species in relation to climate, vegetation, food, habitat and the physiology of the birds. Populations and their movements are studied using a census spanning some ten years, and the history of the Drepaniidae is considered and related to the various ecological factors which have affected the different species.

Barnes, H. F. (1953). The absence of slugs in a garden and an experiment in re-stocking. *Proc. Zool. Soc. Lond.* **123**, 49–58.

Arion reticulatus was introduced to a garden whence it had been exterminated by drought and its subsequent history was followed during three years.

Bensley, C. J. F. (1953). Natural history of the Devil's Punch Bowl. *Rep. Haslemere Nat. Hist. Soc.*

Brief details of a survey of the well-known hollow in the Lower Greensand near Hindhead, Surrey, mainly woodland and heathland, begun in 1950.

Blackwell, J. A. & Dowdeswell, W. H. (1951). Local movement in the Blue Tit. *Brit. Birds*, **44**, 397–403.

Intensive ringing of *Parus caeruleus* at Blundell's School, Tiverton, during three winters disclosed that an expanse of playing fields formed an effective barrier, and that the population density was approximately constant from November to March. The proportion of birds re-captured in subsequent seasons is given.

Blair, C. A. & Groves, J. R. (1952). Biology of the Fruit Tree Red Spider Mite *Metatetranychus ulmi* (Koch) in south-east England. *J. Hort. Sci.* **27**, 14–43.

Life-cycle of *M. ulmi*, and its feeding behaviour. Predator relationships are considered pertaining to five annual generations, and particularly with regard to winter eggs. Developmental stages are identified by the number and situation of the ventral setae.

Braham, A. C., Murgatroyd, J. H., Butler, P. M., Hincks, W. D., Shaw, S. & Steel, W. O. (1954). The entomology of Spurn Peninsula. *Naturalist*, 74–78.

Concludes the Mollusca and deals also with the Crustacea Malacostraca, Myriapoda, fish, Amphibia and reptiles and begins the mammals.

Broadbent, L. (1954). The different distribution of two *Brassica* viruses in the plant and its influence on spread in the field. *Ann. Appl. Biol.* **41**, 174–182.

Suggests that cauliflower mosaic virus is much more widely distributed than cabbage black ring spot because the former occurs in high concentration in the new leaves produced by infected plants, whereas the latter is localized in infected parts of old leaves. Most aphids alight from flight on the upper parts of plants and are therefore much more likely to acquire and transmit cauliflower mosaic than cabbage black ring spot.

Brown, P. E., Davies, M. G. & Mytum, E. (1950). Duration of song of Chiffchaff. *Brit. Birds*, **43**, 153–154.

18 755 song-phrases of less than 15½ s duration were timed, and the result is shown graphically. Half were between 1½ and 5½ s in duration. 24% of songs exceeded 15½ s.

Butt, D. V. & Knipe, P. R. (1950). Black-headed Gulls nesting in trees in West Suffolk. *Brit. Birds*, **43**, 193.

The colony had seven nests, all in trees. Young were reared.

Butt, D. V., Pettitt, R. G. & Vine, A. E. (1950). Great Black-backed Gulls roosting inland. *Brit. Birds*, **43**, 61.

About 450 came to roost together with over 1000 Herring Gulls at Thompson Water, Norfolk, on 6 January, 1949. They were seen in much smaller numbers on other occasions.

Campbell, B. (1950). Breeding of the Pied Flycatcher. *Brit. Birds*, **43**, 13–15.

New facts from observations made in an area of mature oak provided with nestboxes in the Forest of Dean. Data of clutch sizes are given, and the occurrence of second broods is proved.

Campbell, B. (1953). A comparison of bird populations upon 'industrial' and 'rural' farmland in South Wales. *Trans. Cardiff Nat. Soc.* **81**, 4–65.

There has been an impoverishment in the bird population, especially in the remaining semi-natural habitats, due to the industrialization of the South Wales coalfield; but the status of many common species appears to have been relatively stable for possibly fifty years.

Campbell, B. (1954). The breeding distribution and habitats of the pied flycatcher (*Muscicapa hypoleuca*) in Britain. I. The historical and present distribution. *Bird Study*, **1**, 81–101.

First recorded 1676 and found to breed mostly in N. England and N.E. Wales. Between 1850 and 1901 breeding regularly in Wales and S. Scotland and perhaps on Exmoor. Regressed between 1901 and 1939, southern breeding records almost ceasing, but a slight increase occurred in the west. Since 1940 has increased again with many county reappearances and new records. A detailed county survey is included.

Chalke, S. H. (1954). Vertical zonation of some species of birds in oakwood (Eastern Wood Bookham Common). *Lond. Nat.* **33** (1953), 47–51.

Observations on the heights above ground at which six woodland birds were found during winter, with histograms showing for each species the number of occurrences in each of ten vertical zones and the percentage of the total number of occurrences it represents.

Cloudsley-Thompson, J. L. (1953). Diurnal rhythms of locomotory activity in isolated migratory locusts. *Ent. Mon. Mag.* **89**, 233–235.

Isolated adults of *Locusta migratoria migratorioides* in an aktograph tended to be active mostly in the light and at high temperatures. The effect of temperature was largely overridden by that of light, but the rhythm persisted for a few days in constant temperature. Spontaneous activity nevertheless occurred at all hours of the day and night as it does in locust swarms in the field.

Cloudsley-Thompson, J. L. & Sankey, J. H. P. (1953). Some aspects of the fauna of the district around Juniper Hall, Mickleham, Surrey. II. *Ent. Mon. Mag.* **89**, 284–286.

Includes comparative, quantitative lists of the invertebrate fauna of acid and base-rich soils, lists of Arthropods found in association with *Pinus sylvestris* and *Erica cinerea* and of invertebrates found in damp situations and in water, both at Frensham; a list of Coleoptera and Arachnids collected at Mickleham, with observations on the food-plant preferences of *Gryllus campestris* and the response of *Ciniflo ferox* to a vibrating tuning fork by night and by day.

Colyer, C. N. (1954). More about the 'Coffin Fly', *Conicera tibialis* Schmitz (Diptera, Phoridae). *Entomologist*, **87**, 129–132.

A discussion of the stage (probably the adult female or first-stage larva) in which *C. tibialis* enters coffins, based on observations on flies associated with the buried corpse of a dog.

Collyer, E. (1953). The greenhouse red spider mite, *Tetranychus urticae* Koch, on apples in East Anglia. *Rep. E. Malling Res. Sta.* **A 36** (1952), 159–160.

The greenhouse red spider mite has been noticed for the first time in English apple orchards during the past few years, in each case after parathion has been used as an acaricide. Notes are given on the host plants, and a brief outline of the life-history of this potential pest under conditions in Essex.

Collyer, E. (1953). Some predaceous insects of commercial orchards. *Rep. E. Malling Res. Sta.* **A 37**, 218–219.

A brief description and life-history is given of the five predacious insects most abundant in commercial orchards.

Conder, P. J. (1950). On the courtship and social displays of three species of Auk. *Brit. Birds*, **43**, 65–69.

The displays of *Alca torda*, *Uria aalge* and *Fratercula arctica* were observed on Skokholm Island, Pembrokeshire during the summer of 1947.

Crowcroft, P. (1954). The daily cycle of activity in British shrews. *Proc. Zool. Soc. Lond.* **123**, 715–729.

The common shrew has a peak around midnight and one in the mid-morning; the water shrew a peak before sunrise and the pigmy shrew is similar to the common shrew. All three showed superimposed a short period activity of a few hours probably related to feeding rhythms.

Cutcliffe, A. S. (1951). Notes on the breeding habits of the Swift. *Brit. Birds*, **44**, 47–56.

A study over five years of a colony of *Apus apus* at Ilfracombe, Devon, with records of the history of a number of nests, the effects of weather and parasites. Non-breeding adults were present and roosted in empty nests.

Cutcliffe, A. S. (1951). A further note on the breeding habits of the Swift. *Brit. Birds*, **44**, 176–177.

Some 1950 results of observations of a colony already described for 1944–49 (1951, *Brit. Birds*, **44**, 47–56).

Dainton, B. H. (1954). The activity of slugs: 1. The induction of activity by changing temperatures. *J. Exp. Biol.* **31**, 165–187.

Dainton, B. H. (1954). The activity of slugs: 2. The effect of light and air currents. *J. Exp. Biol.* **31**, 188–197.

The main factor is temperature which, between 4 and 20° C, causes increased activity as temperature falls. This can account for observed field behaviour. Humidity has no direct effect, that of illumination is transitory and air currents are avoided.

Davies, M. E. & Edney, E. B. (1952). The evaporation of water from spiders. *J. Exp. Biol.* **29**, 571–582.

Four species were used for experiments on water retention. The tracheae were unimportant; evaporation from lung-books depends greatly on whether they are open. Evaporation from the integument is similar to that from insects in that the effects of temperature and abrasive dusts indicate the presence of a wax layer in the cuticle.

Delany, M. J. (1954). The habitats of the bristle-tail *Petrobius maritimus* (Insecta, Thysanura) on Lundy. *7th Ann. Rep. Lundy Fld Soc.* **1953**, 36–44.

A study of the microhabitats of the insect, always under rocks or stones, on an island in the Bristol Channel.

Delany, M. J. (1954). Studies on the life history and ecology of *Dilta littoralis* (Womersley, 1930) (Thysanura, Machilidae). *Trans. R. Ent. Soc. Lond.* **105**, 31–63.

Details are given of the life-history of this insect based on a quantitative sampling method. Distribution is dealt with under three headings: geographical, plant community relationships and intra-community relationships. The author deals with extrinsic factors maintaining population density: food, the associated fauna and the physical conditions (this last factor is dealt with more fully in: Delany, M. J. (1953, *J. Anim. Ecol.* **22**, 227–239)), and discusses the relative importance of each.

de Worms, C. G. M. (1954). The moths of London and its surroundings. *Lond. Nat.* **33** (1953), 101–146.

Notes on the localities, abundance, food plants and seasonal appearance for the moths, excluding Microlepidoptera, recorded in the London area over some 80 years. It is stated in a preliminary review of some of the more interesting species and of the changes that have taken place in those present, that it is doubtful whether many have entirely disappeared and that there have been a number of recent newcomers.

Dicker, G. H. L. (1952). The biology of the Strawberry Aphid, *Pentatrichopus fragaefolii* (Cock.), with special reference to the winged form. *J. Hort. Sci.* **27**, 151–178.

Two distinct rhythms exist in the annual cycle of the strawberry aphid: on first-year plants the population peak is in late summer or early autumn, and on older plants a peak is reached in May or June followed by a rapid decline. These patterns are related to the number and quality of young leaves produced as a result of fruit development. The behaviour of winged forms and the mode of infestation of strawberry beds are discussed.

Dowdeswell, W. H. & Ford, E. B. (1952). The distribution of spot-numbers as an index of geographical variation in the butterfly *Maniola jurtina* L. (Lepidoptera: Satyridae). *Heredity*, **6**, 99–109.

While the spot pattern of the male Meadow Brown appears to be uniform and approximately symmetrical, in the female the pattern varies between different localities, and there is some evidence of a cline from a bimodal frequency on Tean, Isles of Scilly, through south-west Cornwall to a unimodal pattern between mid-Devon and east Suffolk. The spot pattern on St Martins and Tresco, on either side of Tean, approximates to the west Cornwall type.

Dowdeswell, W. H. & Ford, E. B. (1953). The influence of isolation on variability in the butterfly *Maniola jurtina* L. *Symp. Soc. Exp. Biol.* **7**, 254–273.

Collates data on the spotting pattern of the underside of the hind wing of the Meadow Brown butterfly throughout southern England, the Scillies, Isle of Man and Ireland, and discusses the local variations. Concludes that the frequencies are stabilized by selection.

Downes, J. A. (1953). Notes on the life-cycle of *Xylophagus ater* Mg. (Dipt., Rhagionidae). *Ent. Mon. Mag.* **89**, 136–137.

Deals with food, feeding habits, growth rate and seasonal history.

Duffey, E. (1951). Field studies of the Fulmar *Fulmarus glacialis*. *Ibis*, **93**, 237–245.

Three marked pairs of *Fulmarus glacialis* were observed intensively on Fair Isle for a fortnight in July. The chick does not recognize its parents for the first two or three weeks, and is aggressive when they alight. Brooding periods and feeding are irregular, and at first the chick is probably not fed daily. Chicks were fed on semi-digested animal matter, not on oil.

Edney, E. B. (1954). Woodlice and the land habitat. *Biol. Rev.* **29**, 185–219.

Adaptations include presence of pseudotracheae, suppression of nitrogen metabolism, water absorption by mouth and anus and the development of wide osmotic tolerance—but not regulation. There is no epicuticular wax. Transpiration over short periods reduces effect of heat. A linear order of families relates habitat tolerance to structural adaptation. The importance of behaviour is stressed and topics for further study are listed.

Edwards, G., Hosking, E. & Smith, S. (1950). Reactions of some passerine birds to a stuffed Cuckoo. II. A detailed study of the Willow-Warbler. *Brit. Birds*, **43**, 144–150.

It is concluded that it is the head that provokes aggressive reaction. Stuffed *Accipiter nisus* provoked fear reaction.

Elton, C. S. (1953). The use of cats in farm rat control. *Brit. J. Anim. Behaviour*, **1**, 151–155.

Brings evidence from the study of six rural sites in Berkshire that cats will maintain the immediate areas round farm buildings free from rats, but probably they cannot clear a large initial infestation. The range of control is limited to within about fifty yards of the cat occupied unit. The economics of cat control are outlined.

Foster, J. & Godfrey, C. (1950). A study of the British Willow-Tit. *Brit. Birds*, **43**, 351–361.

Observations on *Parus atricapillus kleinschmidti* in a wood near Oxford in two years, with emphasis on the breeding biology.

Gibb, J. (1950). The breeding biology of the Great and Blue Titmice. *Ibis*, **92**, 507–539.

The result of three seasons' intensive study of populations breeding in nestboxes, with emphasis on quantitative aspects.

Green, J. (1953). The beetles of a Cheshire farm. *Ent. Mon. Mag.* **89**, 81–86.

Lists of beetles found in various habitats on a farm in Cheshire, with a map and information on the topography of the farm and the associated vegetation, crops and vertebrates. Although several species that could become injurious were present, their interactions appear to prevent any one species from becoming too numerous.

Gressitt, J. L. (1953). The coconut rhinoceros beetle (*Oryctes rhinoceros*) with particular reference to the Palau Islands. *Bernice P. Bishop Mus. Bull.* **212**, viii + 157 pp.

A detailed and well-documented exemplification of the basic ecological foundations of methods used in pest control. Discusses the ecology, life history and potential means of control of a beetle introduced into some islands of the Pacific where it has become a very serious threat to coconut plantations.

Grigg, U. M. (1950). Bird skeletons found in a hollow tree. *Brit. Birds*, **43**, 11–13.

Bones of four species of birds found in a hollow tree near Fleet, Hants, were in two layers, and are attributed to death whilst roosting in hard weather, the upper layer with most skeletons to early 1947. The species in order of abundance: *Corvus monedula*, *Columba oenas*, *Sturnus vulgaris*, and *Picus viridis*. More than 130 birds had died in the hollow.

Groves, J. R. (1952). A preliminary account of the summer fruit tortricid, *Adoxophyes orana* (F.R.) in Great Britain. *Rep. E. Malling Res. Sta.* **A 35** (1951), 152–154.

A short account of the occurrence and life-history of the moth *Adoxophyes orana*, a pest of fruit especially of apples, new to Britain.

Guild, W. J. M'L. (1951). Earthworms in agriculture. *Scot. Agric.* **30**, 220–223.

A brief discussion of the effects of earthworm activity in soils, variation in population numbers, and lines of investigation worthy of study from an agricultural viewpoint.

Hewson, R. (1953). The red squirrel—*Sciurus vulgaris leucourus* Kerr in Easter Ross. *Northw. Nat.* (N.S.), **1**, 493–496.

In recent years, numbers have fallen considerably and in 1950 red squirrels were rare in Ross and Sutherland, though in 1951 they were said to be increasing. There is evidence that they also became rare some 100 years ago and subsequently built up, but it is not known whether the present populations are derived from indigenous stock or from stock imported into Inverness in 1844. Destruction by man and tree-felling are not considered responsible for the present decline; population fluctuations on an estate in Easter Ross over the past 50 years, which are shown graphically, are paralleled in Arctic hares, but not rabbits.

Hill, A. R. (1952). Observations on *Lygus pabulinus* (L.), a pest of raspberries in Scotland. *Rep. E. Malling Res. Sta.* **A 35** (1951), 181–182.

Describes damage to raspberry plants by the green capsid *Lygus pabulinus*. No migration of the first generation adults from the host plant was observed over a period of three years in Scotland; apparently different behaviour from that described by some earlier writers who suggest that this species migrates to herbaceous plants in early summer.

Hill, A. R. (1952). The bionomics of *Lampronia rubiella* (Bjerkander), the Raspberry Moth, in Scotland. *J. Hort. Sci.* **27**, 1–13.

Detailed life-cycle of *L. rubiella*, with notes on seasonal behaviour (especially oviposition, hibernation, and feeding habits).

Hill, A. R. (1953). Aphids associated with *Rubus* species in Scotland. *Ent. Mon. Mag.* **89**, 298–303.

Notes on the occurrence of thirteen Aphids on wild and cultivated *Rubus idaeus* and *R. fruticosus* during a survey in ten Scottish counties over a period of six years. Most were breeding species; *Macrosiphum funestum* is recorded from Scotland for the first time. Information on the seasonal occurrence and life history of 3 widespread species and observations on the populations of *Amphorophora rubi*, the commonest species, on leaves of different ages are included.

Howe, R. W. & Burges, H. D. (1953). Studies on beetles of the family Ptinidae. 10—The biology of *Mezium affine* Boieldieu. *Ent. Mon. Mag.* **89**, 217–220.

Data on development and egg production under controlled conditions and observations on survival and increase under warehouse conditions.

Ibbotson, A. & Edwards, C. A. T. (1954). The biology and control of *Otiorrhynchus clavipes* Bonsd. (Rhyn. Coleop.), a pest of strawberries. *Ann. Appl. Biol.* **41**, 520–535.

O. clavipes, a serious pest of strawberries near Cheddar, Somerset, is a voracious feeder. Weevils eat foliage and larvae attack roots and burrow into the rootstock. One egg is laid for every 10 mm^2 of leaf consumed; eggs are both parthenogenetic and fertile, and hatch in about three weeks. Larvae live within the rhizosphere, and travel from plant to plant guided by root exudates.

Jones, A. W. (1954). Notes on the drone-flies (Syrphidae, Diptera) of Wimbledon Common. *Lond. Nat.* **33** (1953), 83–88.

A preliminary systematic list of Syrphids in Volucellinae and Eristalinae noted during 1947–53, with dates, numbers and habitats, and one of plants showing the species attracted to the flowers of each. The data suggest that plant height and flower colour are of little importance in attracting the flies, but all the flowers visited provide a large landing area. The relative scarcity of these Syrphids in heaths may result from a scarcity, not of breeding places, but of attractive plants.

Kennedy, J. S. & Booth, C. O. (1954). Host alternation in *Aphis fabae* Scop. II. Changes in the aphids. *Ann. Appl. Biol.* **41**, 88–106.

Comparison of the feeding preferences and fecundity of different forms of *A. fabae*: apterous and alate virginoparae and gynoparae. All forms prefer the primary host (*Euonymus*) and mature leaves. Findings are discussed in the light of the dual discrimination theory of aphid host selection.

Keywood, K. P. & Melluish, W. D. (1953). A report on the bird population of four gravel pits in the London area, 1948 to 1951. *Lond. Bird Rep.* **17**, 43–72.

Extensive data on breeding and non-breeding summer populations, spring and autumn migrants, resident and visiting species outside the breeding season and congregations and roosts in late summer and autumn at pits in Middlesex, Surrey, Herts and Essex, showing typical local differences and in a control area without gravel pits in Herts, are analysed and discussed. Of the 112 species observed, fifteen nested and nine were winter residents at all the pits; thirteen of the nesting species also breed regularly at other pits in Surrey. Both total breeding populations and populations associated with water were smallest in Surrey, where much of the surrounding area was under cultivation and the sides of the pits steep and lacking in cover. Winter populations were smaller and less varied than summer ones at all the pits. The presence of gravel pits tended to increase the number of species present at all seasons and to lead to slight and moderate increases in summer and winter populations respectively.

Kent, A. K. (1951). Mortality of Chiffchaffs in a snow-storm in Pembrokeshire. *Brit. Birds*, **44**, 64.

Thirteen dead *Phylloscopus collybita* were found in a small copse on 25 April 1950, the second day of heavy snowfall, but none were seen in other copses near.

Kirby, A. H. M. & Gambrill, G. R. (1953). The hatching of summer eggs of the fruit tree red spider mite *Metatetranychus ulmi* (Koch) under artificial conditions. *Rep. E. Malling Res. Sta*, **A 37**, 175–179.

These experiments on the hatching of the summer eggs of *Metatetranychus ulmi* prove that they can hatch in a normal manner under suitable artificial conditions. Good hatches, at about the same rate, were obtained from eggs kept at 24° C in the dark and from eggs kept at laboratory temperature in a north light; but the percentage of eggs hatched was less, and the rate of hatching much lower, from eggs kept at 18° C in the dark.

Lack, D. (1950). The breeding seasons of European birds. *Ibis*, **92**, 288–316.

The value of quantitative measurement is stressed, and examples are given.

Lack, D. (1954). Two robin populations. *Bird Study*, **1**, 14–17.

Discusses variations in robin populations of Marley Wood (Wytham, Oxford) and Dartington (S. Devon), concluding that annual differences at Oxford and habitat differences in Devon are unlikely to be due to territorial behaviour.

Lack, D. & Lack, E. (1951). The breeding biology of the Swift *Apus apus*. *Ibis*, **93**, 501–546.

A study made at Oxford from 1946 to 1951. Weights of adults, eggs and young, incubation and nestling periods, clutch-size and nestling survival, and the frequency of feeding by parents are dealt with, and the profound effect of the weather on all of these. Breeding behaviour is not described in this paper, and feeding habits are only briefly outlined. Much of the field work was done with glass-backed nesting boxes, disturbance being avoided. Resemblance to Procellarii in many aspects of the breeding biology is related to the fact that both groups have safe nesting sites but an uncertain food supply.

Lack, E. (1950). Breeding season and clutch-size of the Wood Warbler. *Ibis*, **92**, 95–98.

Phylloscopus sibilatrix is normally single-brooded in Britain. Breeding is earlier in south Devon than in the central midlands of England. Clutches are smaller in June than in May.

Laurence, B. R. (1953). Some Diptera bred from cow dung. *Ent. Mon. Mag.* **89**, 281–283.

Includes a list of species of twenty-one families bred from cow dung, mostly in open fields, in Hertfordshire.

Lawson, D. F. (1951). Notes on breeding behaviour of Nightjar. *Brit. Birds*, **44**, 281–282.

Sixty hours watching, day and night, and two daily visits at a nest of *Caprimulgus europaeus* from the finding of the first egg until a week after the young had fledged.

Lees, A. D. (1953). Environmental factors controlling the evocation and termination of diapause in the Fruit Tree Red Spider Mite *Metatetranychus ulmi* Koch (Acarina: Tetranychidae). *Ann. Appl. Biol.* **40**, 449–486.

Lees, A. D. (1953). The significance of the light and dark phases in the photoperiodic control of diapause in *Metatetranychus ulmi* Koch. *Ann. Appl. Biol.* **40**, 487–497.

An examination of the effects of photoperiodism, temperature fluctuation, and food availability upon winter-egg (diapause) deposition by *M. ulmi*. Diapause is facultative: over seventy successive summer generations (non-diapause) have been reared under diapause-preventing conditions.

London Natural History Society (1954). Cranford Park Survey. *Lond. Nat.* **33** (1953), 21–22.

This first report of a survey of an area in south-west Middlesex, including marshy woodland, meadowland, a river and an ornamental lake, that was begun in early 1953 includes preliminary lists of birds by A. Anderson and butterflies by C. W. Pierce.

London Natural History Society (1954). The Survey of Bookham Common. Twelfth Year. *Lond. Nat.* **33** (1953). 23–51.

An introductory progress-work includes brief summaries of work in 1953 on the distribution and movement of grasshoppers by W. Ruttledge (p. 23), the grass-inhabiting Hemiptera-Heteroptera of two grass areas by E. W. Groves (pp. 23–24), the occurrence of molluscs in gun-pits and bomb-craters by C. J. F. Bensley (p. 25), and the territories of wrens, yellow buntings and tree pipits by G. Beven (p. 25), as well as several records for Arthropods and a note on the abundance of grey squirrels. The Report also includes a paper on the vertical zonation of birds by S. H. Chalke (pp. 47–51).

Long, D. B. (1954). Factors affecting the larval spot colours of the Emperor Moth, *Saturnia pavonia* L. *Nature, Lond.* **174**, 563.

The spot colour of individual larvae changes progressively throughout the duration of the instar. The change is primarily a response to light intensity. The response appears to be locally determined. The actual colour change involves two components, one occurring in the epidermis, the other in the cuticle.

Mackenzie, J. M. D. (1950). Competition for nest-sites among hole-breeding species. *Brit. Birds*, **43**, 184–185.

Parus major usurped a nest-box occupied by *P. caeruleus*, and reared two *P. caeruleus* chicks with seven of their own. Instances of one species building on the nest of another species are also given.

Mackenzie, J. M. D. (1950). Nestling mortality amongst tits on Tentsmuir, 1949 and 1950. *Brit. Birds*, **43**, 393–398.

On Tentsmuir, an area of windblown sand, mortality was greater than in other areas round Perth, and higher in a broad-leaved wood than in conifers, whereas elsewhere it was least in hardwoods. It is suggested that the poverty of the soil perhaps combined with a population near saturation point, may be the cause.

MacNair, V. J. (1951). Notes on behaviour of Blackbird. *Brit. Birds*, **44**, 99–100.

A female frequented a garden from 1942 till killed by an *Accipiter nisus* in June 1949. Sub-song was frequent in mild weather in October and November, and nest material was sometimes gathered. She was mated to the same male for at least five years.

Massee, A. M. (1952). Transmission of reversion of blackcurrants. *Rep. E. Malling Res. Sta.* **A 35** (1951), 162–164.

Each of twenty-four normal blackcurrant bushes, artificially infested with blackcurrant gall-mites obtained from reverted bushes, developed symptoms of virus disease in three years or less. Controls remained normal and healthy. Similar experiments attempting to transmit reversion by means of currant capsid bug and four species of currant aphids gave negative results.

Massee, A. M. (1953). Notes on some interesting insects observed in 1953. *Rep. E. Malling Res. Sta.* **A 37** 162–167.

Comments on some of the more interesting insects and mites sent to the Station by fruit growers in 1953, with remarks on the damage they cause and suggestions for their control.

May, D. J. & Manning, A. (1951). The breeding cycle of a pair of Wood-Warblers. *Brit. Birds*, **44**, 5–10.

Observations are recorded in diary form from the arrival of the male to the fledging of the young, and the behaviour of *Phylloscopus sibilatrix* during the early stages of the breeding cycle is compared with that of *P. trochilus*.

Miles, M. (1953). Field studies on the influence of weather conditions on egg-laying by the cabbage root fly, *Erioischia brassicae* Bché. I. *Ann. Appl. Biol.* **40**, 717–725.

Warm weather induces heavy egg-laying by the cabbage root fly in the soil around cabbage stems, but in cool, wet and windy weather fewer eggs are laid. Yet infestation in summer is less intense than in spring. Oviposition is not related to the size of adult populations, and it is thought that high temperatures and long hours of sunlight stimulate summer flies to greatest activity when food is most scarce; they do not survive to complete oviposition.

Monk, J. F. (1954). The breeding biology of the greenfinch. *Bird Study*, **1**, 2–14.

Data drawn from British Trust Ornithology nest record cards from 1939 to 1951 and from diaries of the late A. Whitaker (1893–1946). Breeding begins earlier in south-west than in north or south-east England. Average clutch size is just under five, increasing from mid-April to a maximum in the first week of June. There is no evidence of change in size of clutch with latitude. Gives incubation and nestling periods, and discusses breeding success in comparison with other species.

Moore, B. P. (1954). The winter beetle-fauna of an alder log in Surrey. *Ent. Mon. Mag.* **90**, 153.

Beetles of twenty-two species, which are listed, were found immediately beneath the bark in December.

Morley, A. (1950). The formation and persistence of pairs in the Marsh-Tit. *Brit. Birds*, **43**, 387–393.

Observations on a small population of colour-ringed and some unringed *Parus palustris* over five years. Replacements of lost mates took place throughout the year, and pair-formation was linked with territory.

Moreau, R. E. (1951). The British status of the Quail and some problems of its biology. *Brit. Birds*, **44**, 257–276.

It is shown that *Coturnix coturnix* was a familiar bird in Britain at least up to the eighteenth century, but that by the 1860's it was rare. A slight upward tendency began about 1942. The long decline is attributed to human predation rather than changing agricultural practice, and the recovery to protection. Attention is drawn to gaps and conflicting information on the life-history. More than two pages of references are given.

Muir, R. C. (1954). Calling and feeding rates of fledged tawny owls. *Bird Study*, **1**, 111–117.

Analyses food cries of young tawny owls, three broods being watched each for four to five nights, and relates them to time and to degree of hunger. Maximum calling tends to coincide with the main feeding time (around midnight). Unfed chicks call more than do fed ones, and this may induce automatic apportionment of food to the young.

Ogilvie, C. M. (1951). The building of a rookery. *Brit. Birds*, **44**, 1–5.

Observations on the behaviour of *Corvus frugilegus* during the period of intensive building activity at a small rookery.

Owen, D. F. (1951). Nightjars mobbing owls. *Brit. Birds*, **44**, 324.

Breeding *Caprimulgus europaeus* in a Kentish wood mobbed both species of owl, *Strix aluco* and *Athene noctua*, present, and on one occasion a bat, but less aggressively.

Parmenter, L. (1954). City bombed sites survey. The flies of the Cripplegate bombed site, City of London. *Lond. Nat.* **33** (1953), 89–100.

An account of the general ecological conditions and their influence on the dipterous fauna and of the various habitats and ecological niches represented, with the genera and species occupying them. It includes a list of flowers, classified by colour, that are visited by flies, with the species found at them, records of hosts from which parasitic flies have been reared, and a few records of flies preyed upon by spiders and a wasp, together with a systematic list of over 200 flies recorded in the area since 1946.

Peace, T. R. (1954). Experiments on spraying with DDT to prevent the feeding of *Scolytus* beetles on elm and consequent infection with *Ceratostomella ulmi*. *Ann. Appl. Biol.* **41**, 155–164.

Attempts to limit Dutch elm disease by destruction of the beetle vectors *S. scolytus* and *S. multistriatus*; active disease is associated with freshly introduced fungus.

Pearson, R. G. (1954). Observations on the fauna of the umbels of *Heracleum sphondylium*. *Starfish*, **7**, 19–20.

Observations in summer 1953 on hogweed growing in three different habitats in Wiltshire, the fauna consisting entirely of arthropods and mainly of insects.

Pitcher, R. S. (1952). Observations on the Raspberry Cane Midge (*Thomasiniana theobaldi* Barnes). I. Biology. *J. Hort. Sci.* **27**, 71–94.

Pitcher, R. S. & Webb, P. C. R. (1952). Observations on the Raspberry Cane Midge (*Thomasiniana theobaldi* Barnes). II. 'Midge blight', a fungal invasion of the raspberry cane following injury by *T. theobaldi*. *J. Hort. Sci.* **27**, 95–100.

Bionomics of the raspberry cane midge considered as a plantation pest. There are three generations a year, and larvae pupate in the surface soil. Eggs and larvae are sheltered by natural splitting of the cane epidermis, so that the degree of splitting is an important factor in varietal susceptibility. Parasites and predators are recorded. Larval damage affords infection sites for three cane-destroying fungi: *Fusarium culmorum*, *Didymella applanata* and *Leptosphaeria coniothyrium*.

Powne, J. D., Rogers, M. J., Lewis, L. R. & Fincher, F. (1951). Reactions of birds to wasps. *Brit. Birds*, **44**, 405–406.

Two observers record *Parus caeruleus* driven away from food, one records *Phylloscopi* feeding among wasps at *Salix fragilis* exuding sap without interference, and one records *Parus major* taking and eating a *Vespa* sp.

Price, M. Phillips (1950). Influences causing fluctuations of warbler population in cultivated lands and oak woods in the Severn Valley. *Brit. Birds*, **43**, 345–351.

Observations cover the period 1936–1950 for *Phylloscopus collybita* and *P. trochilus*, 1928–1950 for *Sylvia atricapilla* and *S. borin*, and 1927–1950 for *Luscinia megarhyncha*. Increases and declines in numbers are attributed to changes in the vegetation in some instances, but in others the reason is not apparent. A steady decrease in the rabbit population is considered to have resulted in the floor of the oak woods becoming covered with brambles, which has favoured most species but eliminated *Phylloscopus sibilatrix* after 1934.

Rankin, W. T. C. (1950). Blue Tits' reactions to wasps. *Brit. Birds*, **43**, 403.

Parus caeruleus would not alight at food occupied by wasps, and one departed from food when wasps came to it.

Reynolds, J. (1950). Effect of exposure on incubation period and viability of Oystercatcher's eggs. *Brit. Birds*, **43**, 257–258.

Hatching was not appreciably delayed though the eggs had been four times under water, and remained uncovered for ten hours on one occasion.

Scott, H. (1953). A large flight of water-beetles, and their attraction to light. *Ent. Mon. Mag.* **89**, 260–261.

Four species were attracted in large numbers to the lights of a hotel during a very hot, dry spell in July 1952.

Senior, B. J., Sheehy, E. J., O'Sullivan, G. F. & O'Donovan, J. (1953). Blood copper deficiency in Offaly cattle. *Sci. Proc. R. Dublin Soc.* **26** (N.S.), 263–273.

An investigation into cases of unthriftiness and scouring in grazing cattle in Co. Offaly. No cattle with suspected worms or aphosphorosis were used in the investigations. Eighty-seven normal cattle from farms adjacent to the affected area had blood copper figures of 0·07 ml or more per 100 ml, in forty-seven diseased cattle it was 0·04 ml or less per 100 ml. Almost immediate relief was given by a drench of 5 g of copper sulphate. The copper content of the herbage was normal on both the affected and unaffected farms, but the molybdenum content on the affected farms was significantly higher than on those not affected, and it is suggested that in this case the moderate excess of molybdenum is the cause of the disease.

Skead, C. J. (1950). A study of the African Hoopoe. *Ibis*, **92**, 434–463.

The most comprehensive study yet made of any species of *Upupa*. A comment by R. A. Hinde collects references to *Upupa epops* for comparison.

Sneddon, J. L. (1953). Long-tailed field mice: damage to field beans. *Scot. Agriculture*, **33**, 77–78.

An investigation into failures of field bean crops in Killearn brought to light a cause hitherto unsuspected—depredations by *Apodemus sylvaticus*. Damage has also been recorded to barley, wheat, oats, rye, crocus, carnation, and strawberry.

Southern, H. N. & Morley, A. (1950). Marsh-Tit territories over six years. *Brit. Birds*, **43**, 33–45.

A study of a population of four to five pairs *Parus palustris* in a part of Bagley Wood, near Oxford, by colour ringing.

Southern, H. N., Vaughan, R. & Muir, R. C. (1954). The behaviour of young tawny owls after fledging. *Bird Study*, **1**, 101–110.

Records survival and movements of seventy-one tawny owl chicks in Wytham Wood between fledging in mid-May and independence of parents in mid-August. The young birds remain well within the parents' territory and apparently make no attempt to feed themselves. Very few losses occur during this period and mortality must be high afterwards.

Spencer, K. A. (1954). Notes on the British Agromyzidae (Dipt.).—II. *Ent. Mon. Mag.* **90**, 64–65.

Food plants, localities, dates and descriptions of the larval mines for some twelve species new to Britain.

Stratton, L. W. (1954). On *Arianta arbustorum* (L.). *J. Conchol.* **23**, 405–412.

Habitats of a land snail (Helicidae).

Stresemann, E. (1950). Interspecific competition in chats. *Ibis*. **92**, 148.

A note on *Oenanthe oenanthe* establishing its territory in two *O. pleschanka* territories in the Southern Ukraine, and the distribution of *O. oenanthe* and *O. hispanica* on Aegean Sea islands, giving references.

Summers-Smith, D. & Summers-Smith, M. (1950). The nesting of a pair of Spotted Flycatchers. *Brit. Birds*, **43**, 201–204.

The complete nesting cycle was closely observed.

Summers-Smith, D. & Summers-Smith, M. (1951). Starlings attacking Swifts at nest-site. *Brit. Birds*, **44**, 89–90.

Sturnus vulgaris with young under the eaves of a house where in the three previous years both this species and *Apus apus* were known to have bred successfully, attacked the first *A. apus* to arrive in 1950, and kept Swifts away till their young were fledged.

Taylor, C. E. & Johnson, C. G. (1954). Wind direction and the infestation of bean fields by *Aphis fabae* Scop. *Ann. Appl. Biol.* **41**, 107–116.

Shelter and wind direction related to bean infestation by *A. fabae* primary migrants.

Tebbutt, C. F. (1950). Birds becoming 'caught' in flocks of other species. *Brit. Birds*. **43**, 332–333.

An instance of a single *Columba palumbus* following the evolutions of a flock of *Anas platyrhyncha*, and of three *A. crecca* following the manœuvres of a flock of *Calidris alpina*.

Thomas, D. C. (1954). Notes on the biology of some Hemiptera Heteroptera. *Entomologist*, **87**, 25–30.

Records of some Heteroptera found in arable fields in Devon and Cornwall, mostly associated with weeds, with observations on the habits, food plants and life-cycles of two Cydnids and three Pentatomids.

Thomson, A. L. (1950). Factors determining the breeding seasons of birds: an introductory review. *Ibis*, **92**, 173–184.

A discussion of six original papers on breeding seasons in different parts of the world.

Thompson, H. V. (1953). The edible dormouse (*Glis glis* L.) in England, 1902–1951. *Proc. Zool. Soc. Lond.* **122**, 1017–1024.

Distribution in Europe and, since its introduction, in Britain. Notes on habits and its insignificant status as a pest are followed by the recommendation that it should not be further introduced.

Tucker, R. C. (1951). Putting back the clock. The story of a deer forest. *Scot. Agric.* **31**, 73–75.

The Forest of Killilan, transformed from sheep country to deer forest in 1880, was returned to sheep in 1940. The hills now carry a permanent sheep stock, but deer are still present.

Wallace, H. R. (1953). Notes on the biology of *Plastosciara pernitida* Edwards and *Plastosciara schineri* Winnertz (Dipt., Sciaridae). *Ent. Mon. Mag.* **89**, 118–120.

Observations on the life-history, feeding habits, growth and reactions to temperature and humidity of specimens collected on pine stumps in Lancashire and reared in captivity.

Warren, R. B. (1954). The effects of the east coast floods on the bird life of Essex. *Essex Bird Rep.* **1953**, 44–45.

Notes on the effects of the great flood of January/February 1953.

Watson, M. A. & Nixon, H. L. (1953). Studies on the feeding of *Myzus persicae* (Sulz.) on radioactive plants. *Ann. Appl. Biol.* **40**, 537–545.

Adult apterae of *M. persicae* feeding on turnip and sugar-beet leaves take up 10 μg of sap for the first hour of feeding (probably before the phloem is reached) and 40 μg per hour in the next three hours. Starved aphids may feed on tissues other than phloem.

Way, M. J., Smith, P. M. & Potter, C. (1954). Studies on the bean aphid (*Aphis fabae* Scop.) and its control on field beans. *Ann. Appl. Biol.* **41**, 117–131.

Aphid control immediately after primary migration to beans has ceased prevents build-up of destructive populations.

Welch, A. (1951). Birds becoming 'caught' in flocks of other species. *Brit. Birds*, **44**, 405.

The parents of a late brood of *Carduelis cannabina* which had appeared increasingly casual in attending the nest, eventually deserted by joining a passing flock of *Anthus pratensis* which alighted for a few minutes nearby.

Williamson, K., Rogers, M. J., Arnold, G. A., Arnold, M. A., Gribble, F. C., Robson, R. W. & Hickling, R. A. O. (1951). Birds becoming 'caught' in flocks of other species. *Brit. Birds*, **44**, 197–201.

A number of instances are given by seven separate observers, a variety of species being involved.

Wood, C. A. (1950). The strawberry aphid, *Pentatrichopus fragariae* (Theob.), in North Wales, with special reference to the maintenance of healthy strawberry stocks in non-fruit-growing areas. *J. Hort. Sci.* **26**, 22–34.

Includes population studies of *P. fragariae* in relation to winter survival, and parasitism of the aphis by the fungus *Empusa planchoniana*. Summer migration of alatae occurs whenever populations are large.

Woodroffe, G. E. (1953). The cinder-patch—an interesting artifical habitat. *Middle-Thames Nat.* **6**, 21–23.

A review of the ecological conditions provided by old cinder-tips and notes on the habits of the Lygaeids, Coreids, Neids and Mirids found on two such sites in Buckinghamshire.

Woodroffe, G. E. (1953). An ecological study of the insects and mites in the nests of certain birds in Britain. *Bull. Ent. Res.* **44**, 739–772.

The insect fauna includes twelve species listed as ectoparasites of birds, sixty-six scavenger species and fourteen predatory species. Mites included one ectoparasite, ten scavengers and eleven predators. Frequency of occurrence of the more important species is stated and their abundance estimated. Nests examined were chiefly those of house sparrow, house martin, city pigeon, jackdaw and swallow, but nests of many other birds were also studied. Two distinct types of nest are recognized, the wet nest exposed to rain and the dry nest in shelter: the dry nest fauna is particularly discussed. The influence of nest composition, internal temperature and humidity upon the fauna are considered, as also are predator-prey relationships existing between members of the fauna; methods of nest colonization by different members of the fauna are discussed. A little-known study of the same subject by S. Nordberg (1936) is fully reviewed and discussed.

Woodroffe, G. E. (1954). An additional note on the fauna of birds' nests in Britain. *Bull. Ent. Res.* **45**, 135–136.

Specimens recorded (Woodroffe, 1953, *Bull. Ent. Res.* **44**, 739–72) as *Ptinus subpilosus* are *P. fur*, and *P. hirtellus* is added to the previous list. *Glycphagus* n.sp. of the previous list is probably *G. geniculatus* Vitz. The only species of *Ptinus* amongst those recorded which is capable of colonizing nests by flight is *P. sexpunctatus*. Females of the other species recorded normally have vestigial wings, although males of three of them have fully developed wings.

Woods, H. E. (1950). Notes on the breeding habits of the Corn-Bunting in Hampshire. *Brit. Birds*, **43**, 82–83.

Summarizes a close study of over fifty nests made in three seasons.

Yapp, W. B. (1953). The bird community of the Fell woods of the English Lake district. *Northw. Nat.* (N.S.) **1**, 503–512.

The seven isolated, deciduous woods at altitudes exceeding 1000 ft studied, which constitute an ecotone of the first order, contained a highly characteristic bird community, of which all are strict insect-feeders, and most nest regularly or occasionally on the ground, are somewhat northern in distribution, and show a tendency to increased relative length of tarsus. There was an almost complete emigration in autumn, and tits were the only regular inhabitants during winter. The emigration of chaffinches from semi-natural oak and birch woods is probably general for England, except where proximity to houses renders it unnecessary.

Yeates, G. K. (1950). Field notes on the nesting habits of the Great Northern Diver. *Brit. Birds*, **43**, 5–8.

Observations made in Iceland in June of 1948 and 1949, too late for courtship display, but three forms of display are described. Eleven photographs include two of the breeding habitat.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Bailey, C. E. G. (1950). Towards an orthography of bird song. *Ibis*, **92**, 115–122.

The development of the sound spectrograph, and its use in recording bird songs are described.

Barnes, H. (1953). Considerazioni statistiche sulla distribuzione spaziale di alcuni organismi planctonici raccolti su un lungo percorso nel Golfo della Clyde. *Mem. Ist. Ital. Idrobiol. de Marchi*, **7**, 109–127.

A statistical comparison between a series of plankton hauls made in the Firth of Clyde by day with a series taken by night. The mean of catches by day and by night did not differ significantly, except for those species known to make vertical migrations. The spatial relations over the area are considered in relation to the type of organism and its dispersal.

Barnes, H. (1953). A simple and inexpensive closing net. *Mem. Ist. Ital. Idrobiol. de Marchi*, **7**, 189–198.

A simple and inexpensive net for taking vertical plankton hauls is described.

Barnes, H. (1953). A note on cumulative frequency curves. *Mem. Ist. Ital. Idrobiol. de Marchi*, **7**, 201–207.

Size measurements on copepod populations, when plotted as a cumulative curve on probability paper, show a 'falling off' from a straight-line relationship. This phenomenon is discussed.

Beverton, R. J. H. (1953). Some observations on the principles of fishery regulation. *J. Cons. Int. Explor. Mer*, **19**, 56–68.

Dynamics of plaice and haddock populations in the North Sea.

Boase, H. (1950). Calls of Tawny Owls. *Brit. Birds*, **43**, 86.

A wide range of calls are briefly described.

Chiswell, J. R. (1954). *Tipula livida* v.d.Wulp (Diptera, Tipulidae) new to Britain. *Entomologist*, **87**, 124–126.

This Tipulid was reared in March–April from larvae in leaf mould and soil in woods near Bristol. The larvae also occurred in a beech wood in Wiltshire. A description of the adult is given, with an amendment to the appropriate couplet in Coe's Key, and characters distinguishing it from other British species.

Cole, H. A. & Mistakidis, M. N. (1953). A device for the quick and accurate measurement of carapace length in prawns and shrimps. *J. Cons. Int. Explor. Mer*, **19**, 77–79.

Adaptation of standard screw-micrometer.

Collin, J. E. (1954). The genus *Chiastochaeta* Pokorny (Diptera: Anthomyiidae). *Proc. R. Ent. Soc. Lond.* (B) **23**, 95–102.

A table is provided for distinguishing males of *Chiastochaeta*.

Collyer, E. (1953). The effect of spraying materials on some predatory insects. *Rep. E. Malling Res. Sta.* **A 36** (1952), 141–145.

An investigation into the effect of sprays on the more important predators of the fruit tree red spider mite. Summer spraying, particularly with DDT, BHC and parathion, appears to cause the most severe mortality among all these predators. Routine winter oil-washes, although killing some adults of several hibernating species, do not appear to affect the eggs of the black-kneed capsid *Blepharidopterus angulatus*.

Conder, P. J. & Keighley, J. (1950). The leg colouration of the Willow-Warbler and Chiffchaff. *Brit. Birds*, **43**, 238–240.

The examination of 426 *Phylloscopus trochilus* and 36 *P. collybita* at Skokholm Bird Observatory leads to the conclusion that there is considerable overlapping in the leg colour.

Crosse, J. E. & Pitcher, R. S. (1953). A preliminary note on methods for obtaining bacteria-free eelworms. *Rep. E. Malling Res. Sta.* **A 36** (1952), 138–140.

The best results, in experiments to obtain viable bacteria-free eelworms *Aphelenchoides ritzema-bosi* using chemical sterilants, were achieved by immersion in low concentrations of ethoxyethyl mercury chloride for periods up to 90 h.

Dales, R. P. (1953). A simple trap for Tipulids (Dipt.). *Ent. Mon. Mag.* **89**, 304.

Many thousands of tipulids were trapped in empty hollow, truncated cones used for storing sand on a miniature golf course. If trapped insects were removed promptly, while still alive, a more accurate idea of population density might be obtained from the numbers caught in such a trap than in traps making use of attractants.

Dicker, G. H. L. (1953). The apple, pear, and quince aphids. *Rep. E. Malling Res. Sta.* **A 37**, 213–217.

A simple guide for the field identification of the common aphids of apple, pear and quince. Simple characters are tabulated and biological notes appended for each species considered.

Doncaster, J. P. (1954). Notes on the genus *Lipaphis* Mordvilko, 1928 (Homoptera: Aphididae) and description of a new species. *Proc. R. Ent. Soc. Lond.* (B) **23**, 83–88.

Includes a key to the species of *Lipaphis*.

Forster, G. R. (1954). Preliminary note on a survey of Stoke Point rocks with self-contained diving apparatus. *J. Mar. Biol. Ass. U.K.* **33**, 341–344.

A survey, using self-contained compressed-air diving apparatus, of the sub-littoral rock fauna in a locality off the S. Devon coast. The survey extends below the *Laminaria* belt, to a total depth of 24 m.

Gibson, F. A. (1953). Tagging of Escallops (*Pecten maximus*, L.) in Ireland. *J. Cons. Int. Explor. Mer*, **19**, 204–208.

Development of satisfactory marking method allowing study of shell ring formation.

Gibson, J. A. (1950). Methods of determining breeding-cliff populations of Guillemots and Razorbills. *Brit. Birds*, **43**, 329–331.

Two methods are described, but considered unsuitable; a method using a control group, and counts of incubating birds are suggested as giving satisfactory results.

Grant, C. H. B. & Mackworth-Praed, C. W. (1952). On the species and races of the yellow wagtails from Western Europe to Western North America. *Bull. Brit. Mus. (Nat. Hist.) (Zool.)* **1**, 253–268.

Recognizes seven species, the characters and known distributions of which are described.

Hartley, P. H. T. (1954). Back garden ornithology. *Bird Study*, **1**, 18–27.

A salutary summary of the advantages of studying birds in gardens. Hints on layout, screening etc., and on experimental lures and models.

Haskell, P. T. & Ives, D. G. (1954). A culture method for *Acheta domestica* (L.) (Orth., Gryllidae). *Ent. Mon. Mag.* **90**, 94–95.

Hickin, N. E. (1954). Larvae of the British Trichoptera. 41. *Stenophylax latipennis* Curtis (Limnophilidae). *Proc. R. Ent. Soc. Lond.* (A) **29**, 55–58.

The larva is described and figured. The adult is figured.

Hickin, N. E. (1954). Larvae of the British Trichoptera. 42. *Rhyacophila septentrionalis* Mclachlan (Rhyacophilidae). *Proc. R. Ent. Soc. Lond.* (A) **29**, 59–61.

The larva is described and figured. The adult is figured.

Kay, G. T. (1950). The Iceland Gull in winter. *Brit. Birds*, **43**, 399–402.

Descriptions of *Larus glaucoides* observed round the Shetlands in the winter of 1949/50 showing how the age of birds in their first four winters can be recognized.

Kerrich, G. V. (1952). A review, and a revision in greater part, of the Cteniscini of the Old World (Hym., Ichneumonidae). *Bull. Brit. Mus.* (*Nat. Hist.*) (*Ent.*) **2**, 305–460.

A taxonomic review of the group with illustrated descriptions, including two new generic names and ten new species. A key to the Old World species is included.

LeQuesne, W. J. (1945). Studies on the British species of *Anthocoris* Fallén (Hem., Anthocoridae) including two new subspecies. *Ent. Mon. Mag.* **90**, 36–40.

Includes a key to the British species.

Meinertzhagen, R. (1951). Some relationships between African, Oriental, and Palaearctic genera and species, with a review of the genus *Monticola*. *Ibis*, **93**, 443–459.

The aim of the paper is 'to broaden the bases of genera and species occurring in the Palaearctic Region by lifting taxonomy out of the narrow rut of regional ornithology'. Examples of wide distributional gaps include those between some European species and their representative races in East Asia and North America. The writer indicates when races occurring in the region distant from the main area of the species are not accepted as such by other authorities.

Miles, P. M. (1954). A trap designed to collect insects attracted by 'sugar'. *Ent. Mon. Mag.* **90**, 86–87.

Nicholson, A. J. (1954). Experimental demonstrations of balance in populations. *Nature, Lond*, **173**, 862–863.

Controlled experiments with *Lucilia cuprina* show that compensatory reaction to density change is a feature of a stable population system.

North, M. E. W. (1950). Transcribing bird-song. *Ibis*, **92**, 99–114.

Suggests a field method which is accurate and minimizes errors.

Perkins, J. F. (1953). Notes on British Ichneumoninae with descriptions of new species (Hym., Ichneumonidae). *Bull. Brit. Mus.* (*Nat. Hist.*) (*Ent.*) **3**, 105–176.

Additions to and deletions from Kloet & Hincks' *Check List of British Insects* (1945), with descriptions of two new genera and sixteen new species. A revision of the nomenclature and a check list of the British species of Ichneumoninae.

Poulding, R. H. (1951). The use of extruded plastic for colour marking. *Brit. Birds*, **44**, 126–127.

A technique using tubing of polyvinyl chloride extruded plastic for ringing juvenile *Larus argentatus* and *L. fuscus* proved satisfactory. A visual record of a *L. argentatus* was obtained 19 months after ringing. Two methods of attaching the rings are given.

Sell, C. N. G. (1954). Observations with a mercury vapour light-trap. *Starfish*, **7**, 17–19.

Notes on moths and other animals attracted to the trap on two evenings in October 1953, at Bishop's Stortford, Herts. For one evening the times of capture of each of the 17 species caught is analysed in three periods from 1830 to 0400 h.

Smith, W. & McIntyre, A. D. (1954). A spring-loaded bottom-sampler. *J. Mar. Biol. Ass. U.K.* **33**, 257–264.

A new type of grab, sampling 1/10 m^2 is described. It is designed for use on sandy bottoms, and can be used in rough sea conditions.

Spence, T. (1954). A taxonomic study of the females of the British *Lucilia* species (Diptera: Calliphoridae). *Proc. R. Ent. Soc. Lond.* (B) **23**, 29–35.

A key is provided.

Spencer, K. A. (1953). Notes on the British Agromyzidae (Dipt.). I. *Ent. Mon. Mag.* **89**, 296–297.

The identity of 58 species on the British list, which are enumerated, was confirmed by breeding. Some additions to the list are also included with food plants and localities.

Spooner, G. M. (1954). Notes on species of *Omalus* (Hym., Chrysididae) including one new to the British list. *Ent. Mon. Mag.* **90**, 135–138.

Includes a key to the five British species, the distribution in Britain of each, and notes on the distinguishing characters and habitats. The addition to the British list is *O. punsticollis*.

Stelfox, A. W. (1954). New species of Dacnusinae (Hym., Braconidae) from Ireland. *Ent. Mon. Mag.* **90**, 159–165.

The species here described are *Dacnusa crassipes*, *D. rufimarginata*, *D. coracina*, *D. obesa*, *D. fasciata* and *D. nigropygmaea*.

Stokes, B. M. (1953). Biological investigations into the validity of *Contarinia* species living on the Cruciferae, with special reference to the Swede Midge, *Contarinia nasturtii* (Kieffer). *Ann. Appl. Biol.* **40**, 726–741.

Fourteen additional host plants are recorded for *C. nasturtii* which is shown to be synonymous with *C. isatidis* and *C. ruderalis*. The varied gall forms on leaves and inflorescences of crucifers are discussed and illustrated.

Tchan, Y. T. & Bunt, J. S. (1954). Direct microscopy for study and count of soil Protozoa. *Nature, Lond.* **174**, 656.

A differential staining technique is described which makes possible a direct count of bacteria, fungi and protozoa against a background of soil particles.

Thompson, H. V. (1953). Experimental live trapping of rats, with observations on their behaviour. *Brit. J. Anim. Behaviour*, **1**, 96–111.

Contains useful data on different types of live traps for rats, with analyses of their efficiency based on direct observations of rats entering and leaving them.

Van Emden, F. L. (1953). On the taxonomy of Rhynchophora larvae: Adelognatha and Alophinae (Insecta: Coleoptera). *Proc. Zool. Soc. Lond.* **122**, 651–795.

This most important taxonomic work permits the identification of weevil larvae. The usual classification of the adults is not entirely supported by the affinities of larval morphology.

Wickstead, J. (1953). A new apparatus for the collection of bottom plankton. *J. Mar. Biol. Ass. U.K.* **32**, 347–355.

Description of a net which samples plankton from the immediate vicinity of the sea bottom, the net being open only when in contact with the bottom.

3. PARASITES

Allan, R. M. (1953). A further record of the flea *Tarsopsylla octodecimdentata* (Kol.) in Scotland. *Scot. Nat.* **65**, 192–193.

A female flea taken on the red squirrel in Aberdeenshire. Two squirrel fleas of different species were taken on the bank-vole.

Clarke, A. S. (1954). Studies on the life cycle of the pseudophyllidean cestode *Schistocephalus solidus*. *Proc. Zool. Soc. Lond.* **124**, 257–302.

The life-cycle through stickleback and *Cyclops* was followed in field and laboratory; growth rates of stages were measured and the weights of host and parasite measured through the year. *Cyclops* is an unimportant part of the diet of the fish.

Clay, T. (1951). The Mallophaga and relationships within the Falconiformes. *Ibis*, **93**, 628.

The suggestion of Mayr and Amadon (1951, *Amer. Mus. Nov.* No. 1496) that *Sagittarius* and the Cathartae may not be related to the rest of the Falconiformes is not supported by an examination of the Mallophaga that parasitize them, three genera or species groups, including *Falcolipeurus* which is found only on Falconiformes, being common to Falcones and Cathartae.

Duddington, C. L. (1954). Nematode-destroying fungi in agricultural soils. *Nature, Lond.* **173**, 500–501.

A list of 20 named fungi is provided.

Hough, J. S. (1953). Studies on the common spangle gall of oak. I. The developmental history. *New Phytol.* **52**, 149–177.

Largely devoted to observations on the reactions of the plant tissues to larval attack. Some notes on the orientation of the larva within the bilaterally symmetrical gall.

Morgan, D. O., Parnell, I. W. & Rayski, C. (1952). Worm infestations in Scottish hill sheep. *Scot. Agric.* **32**, 46–53.

Seasonal fluctuations of worm populations in hill sheep, especially species of *Ostertagia*, *Trichostrongylus*, and *Nematodirus*.

Oppenheimer, Carl H. (1953). Why study marine fish diseases? *J. Cons. Int. Explor. Mer*, **19**, 39–43.

Disease as a cause of mortality in fish stocks.

Rothschild, M. (1952). A collection of fleas from the bodies of British birds, with notes on their distribution and host preferences. *Bull. Brit. Mus.* (*Nat. Hist.*) (*Ent.*) **2**, 187–232.

143 specimens of ten species of flea taken from thirty-six species of British birds. For the first time it is possible to begin discussing the geographical distribution and host preferences of some species of bird fleas. Fleas do not occur on birds only during the breeding season, but throughout the year.

Simmonds, F. J. (1953). Observations on the biology and mass-breeding of *Spalangia drosophilae* Ashm. (Hymenoptera, Spalangiidae) a parasite of the frit-fly, *Oscinella frit* (L.). *Bull. Ent. Res.* **44**, 773–778.

In the field in Canada the parasite is efficient in destroying frit puparia. The parasite is so far unknown in England, but it might prove an effective controlling agent of the frit fly if introduced; the life-history of the parasite has been studied with a view to its introduction to England. A technique for mass-breeding of the parasite on puparia of *Drosophila melanogaster* is described.

Simmons, K. E. L. (1950). A Buff-backed Heron incapacitated by *Mallophaga*. *Ibis*, **92**, 648.

Smit, F. G. A. M. (1953). Notes on the flea *Nosopsyllus londiniensis* (Rothschild) (Siphon., Ceratophyllidae) in Great Britain. *Ent. Mon. Mag.* **89**, 255–257.

Information on the distribution, hosts and means of dispersal of this introduced species.

Stinson, N. E. (1954). Occurrence of *Diplozoon paradoxum* Nordmann on the gills of Rudd *Scardinius erythrophthalamus* (L.) from Co. Tyrone. *Irish. Nat. J.* **11**, 234.

Stone, L. E. W. (1953). Observations on the occurrence of the eelworm, *Pratylenchus pratensis* Filipjev, in delphinium roots. *Ann. Appl. Biol.* **40**, 742–749.

P. pratensis is associated in the West Country with delphinium root lesions and rot. It can persist in the soil for 12 years, but has not yet been found associated with root damage to other cultivated plants.

Taylor, E. L. (1954). Grazing behaviour and helminthic disease. *Brit. J. Anim. Behav.* **2**, 61–62.

A brief, suggestive, summary of observations on grazing behaviour of horses, cattle, sheep and goats, with particular reference to the tendency of each animal to avoid grazing close to faeces from its own kind. Infers that this may be an important factor in the epidemiology of helminth infections.

Thomlinson, J. R. (1953). Disease among Border sheep. A further survey in the Sourhope district—Part I. *Scot. Agric.* **33**, 78–83.

Includes monthly counts of worm eggs in faeces of free-ranging sheep in the Cheviots.

Thompson, G. B. (1953). The parasites of British birds and mammals. XXV. Additional notes on *Crataerina pallida* (Latr.) (Dipt., Hippoboscidae). *Ent. Mon. Mag.* **89**, 208–209.

Effect on host, correlation of life-cycle with that of the host, and means of dissemination, based on observations on swifts' nests in Devon.

Thompson, G. B. (1953). The parasites of birds and mammals. XXVI. Further notes on sand martins' fleas. *Ent. Mon. Mag.* **89**, 224–226.

Deals with the life-cycle, survival during flooding and the absence of the host, and dissemination of *Ceratophyllus styx*.

Thompson, G. B. (1954). The parasites of British birds and mammals. XXVII. Some notes on *Ceratophyllus borealis* Rothschild (1907) (Siphonaptera). *Ent. Mon. Mag.* **90**, 4–9.

Summarizes the distribution in England and hosts, and contains a detailed account of the life-cycle, host relationship, and numbers per nest, based on data from wheatears' nests on Skokholm.

4. FOOD AND FOOD HABITS

Armstrong, D. G. & Thomas, B. (1953). Tethered sheep for moorland experiments. *Scot. Agric.* **32**, 150–152.

Describes the use of sheep tethered by 15 ft ropes in an attempt to assess the value of common heather (*Calluna vulgaris*) as sheep feed. Only tips of average length $\frac{3}{4}$ in. were eaten; in the case of old heather these tips represented a season's growth. When tethered on ground with 50 % cover of four year old heather, the remainder of the vegetation being *Nardus stricta*, *Festuca ovina* and *Juncus squarrosus*, the *Juncus* was the preferred food.

Barnes, H. F. (1953). Investigations into the gall midges of chrysanthemum flowers, 1951–53. *Entomologist*, **86**, 292–297.

Includes preliminary information on the bionomics and distribution in Britain of seven gall midges from the flowers of wild *Chrysanthemum leucanthemum* and lists of the cultivated species and varieties in which each has been found or has been reared under experimental conditions. Four feed on the flowers, but only *Contarinia chrysanthemi* is harmful; of the others, one preys on aphids, another on other gall midges or mites, and the third lives as an inquiline.

Blezard, E. (1954). Food of birds. *Trans. Carlisle Nat. Hist. Soc.* **8**, 75–101.

Detailed records of the food of ninety-three species in Lakeland, based on field observations and stomach contents.

Collyer, E. (1952). Biology of some predatory insects and mites associated with the Fruit Tree Red Spider Mite (*Metatetranychus ulmi* (Koch)) in south-eastern England. I. The biology of *Blepharidopterus angulatus* (Fall.) (Hemiptera-Heteroptera, Miridae). *J. Hort. Sci.* **27**, 117–129.

The black-kneed capsid, *B. angulatus*, is the principal predator of the red spider mite in commercial orchards, although it is partly phytophagous. Life stages are described. Eggs laid in late summer hatch in the following May, June or July.

Cott, H. B. (1953). The palatability of the eggs of birds: illustrated by experiments on the preferences of the ferret (*Putorius furo*) and cat (*Felis catus*); with notes on other egg-eating Carnivora. *Proc. Zool. Soc. Lond.* **123**, 123–141.

Results with these predators are similar to those previously obtained with other animals.

Cott, H. B. (1954). The palatability of the eggs of birds: mainly based upon observations of an Egg Panel. *Proc. Zool. Soc. Lond.* **124**, 335–463.

Includes a list of 212 species arranged in order of palatability and data on size, colour, etc., of eggs.

Dicker, G. H. L. (1952). Studies in population fluctuations of the strawberry aphid, *Pentatrichopus fragaefolii* (Cock.) 1. Enemies of the strawberry aphid. *Rep. E. Malling Res. Sta.* **A 35** (1951), 166–168.

The strawberry aphid is on rare occasions parasitized by *Aphidus* sp. and *Aphelinus asychis*, more frequently by the fungus *Empusa planchoniana*, apparently in warm, humid weather. Of the sixteen insects and mites listed as predators only *Anthocoris nemorum*, *Tachyporus hypnorum* and *T. obtusus* occur regularly on the strawberry. No correlation between the population fluctuations observed in the strawberry aphid and its predators has yet been established.

Dunn, J. A. (1954). *Micromus variegatus* Fabricius (Neuroptera) as a predator of the pea aphid. *Proc. R. Ent. Soc. Lond.* (A) **29**, 76–80.

Field and laboratory observations show that the larvae of this lacewing play an important role as predators in the control of the pea aphid (*Acyrthosiphon pisum*).

Elkin, H. W. (1954). Notes on food of whiting, *Gadus merlangus* L. *Irish Nat. J.* **11**, 183–187.

Stomach contents of 1438 whiting from the east and west coasts of Ireland proved broadly similar, the favoured foods being Crustacea and fish, followed in the west by Polychaetes and Mollusca, and in the east by many fewer Polychaetes and Nematodes.

Gardner, A. E. (1954). Odonata with prey. *Entomologist*, **87**, 139.

Enallagma cyathigerum with *Glyphipterix thrasonella*, *Graphocephala coccinea* and *Pilaria adjuncta*, and *Coenagrion puella* with *Ptychoptera contaminata*.

Gradwell, G. R. (1953). Prey of *Calosoma* [recte *Carabus*] *clathratus jansoni* Kraatz (Col., Carabidae) in Sutherland. *Ent. Mon. Mag.* **89**, 78.

Adults feeding on larvae of the oak eggar moth, *Lasiocampa quercus*.

Hughes, A. M. (1952). A new Glycyphagid mite—*Caproglyphus munroi*. *J. Linn. Soc.* (*Zool.*) **42**, 168–175.

Feeding on dead insects in disused spider webs in Surrey.

Hunter, W. R. (1954). *Valvata piscinalis* (Müller) used by *Phryganea* in Loch Lomond. *J. Conchol.* **23**, 402–403.

Caddis larvae using a freshwater gastropod as both food and material for making their cases.

Kidd, L. N. (1954). *Aeshna grandis* preying upon *Apis mellifera*. *Entomologist*, **87**, 148.

Laurence, B. R. (1954). *Limnophora riparia* Fall. (Dipt., Muscidae) sucking insect juices. *Ent. Mon. Mag.* **90**, 31.

A female feeding on a dead female *Chironomus* on the surface film of Malham Tarn.

Le Gros, A. E. (1954). A note on dragonflies as prey of spiders. *Lond. Nat.* **33** (1953), 3–4.

Dragonflies' wings were found on the retreats of six of 31 webs of *Araneus cornutus*. The species concerned were *Lestes sponsa*, with one *Sympetrum striolatum*. In experiments, *Coenagrion puella* escaped with difficulty from webs of *A. cornutus* and were usually attacked by the spider, whereas *S. striolatum* quickly freed themselves and the spider made no response. *Enallagma cyathigerum* and *Agrion virgo* have also been observed as prey of *A. cornutus*, which probably kills many zygopterids each year.

LeQuesne, W. J. (1954). *Psallus salicellus* Meyer-Duer (Hem., Miridae) on bramble. *Ent. Mon. Mag.* **90**, 21.

An unusual food-plant.

Meiklejohn, M. F. M. (1954). The food of the Scarlet Grosbeak. *Scot. Nat.* **66**, 55–56.

A bird watched on the Isle of May in the Firth of Forth in September 1952 ate the seeds of sow-thistles, *Sonchus arvensis* and *S. asper*.

Moore, B. P. (1953). Some records of dragonflies with their prey. *Ent. Mon. Mag.* **89**, 94.

Records for eleven species.

Parmenter, L. (1953). Some spiders and their prey. *Ent. Mon. Mag.* **89**, 135.

Records of prey (almost entirely dipterous) for eleven spiders, with dates and localities.

Pitcher, R. S. (1953). The host plant range and economic importance of a group of gall midges (*Thomasiniana* spp.) associated with fruit. *Rep. E. Malling Res. Sta.* **A 37**, 168–170.

A comparison is made of all the members of the genus *Thomasiniana* at present known from Rosaceous host plants, including a newly described one from wild blackberry. From host plant preference trials there appear to be two strains within the present species *T. oculiperda*, favouring apple and rose respectively.

Prevett, P. F. (1954). Fauna of a dead pheasant in London, S.E. 27. *Ent. Mon. Mag.* **90**, 3.

Nine beetles and two clothes moths associated with the dry head, wings and feet.

Smith, D. (1954). Larval food plants of *Melitaea athalia*. *Entomologist*, **87**, 86.

Nepeta nervosa, *Veronica spicata*, *Linaria purpurea* and foxgloves, in a garden in Essex.

Stroyan, H. L. G. (1954). A prey record for *Chrysopa albolineata* Killington (Planipennia). *Entomologist*, **87**, 147.

A fully grown larva preying upon *Cinara laricicola* on larch.

Wells, T. P. (1950). 'Anting' of Carrion Crow. *Brit. Birds*, **43**, 402.

Corvus corone observed at an ants' nest for half an hour, probably the second record of this for the species.

5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION

Note. In view of A. A. Massee's proposal to produce a revised list of British Hemiptera Heteroptera, the numerous local records relating to this group published in *Ent. Mon. Mag.* have not been abstracted.

Alexander, W. B. (1950 & 1951). The index of Heron population, 1949; 1950. *Brit. Birds*, **43**, 78–80; **44**, 123–126.

Reports of 162 heronries in the British Isles were received in 1949, and of 207 in 1950. The index of population rose from 57 in 1948 to 77 in 1949, and 94 in 1950, compared with 100 for normal years, 1928 and 1936–1939 inclusive. Recovery after the severe winter 1946/47 was not evident till 1949. In the report for 1950 a graph shows the indices of population and the mean temperature of the coldest winter month (at Norwich) from 1928.

Allen, A. A. (1954). *Epuraea terminalis* Man. (Col., Nitidulidae) new to southern England. *Ent. Mon. Mag.* **90**, 82.

In Kent and Berkshire.

Allen, A. A. (1954). *Atomaria lewisi* Reit. (Col., Cryptophagidae) in Surrey, Berks., and Oxon. *Ent. Mon. Mag.* **90**, 96.

New county records.

Allen, R. H. (1953). Bird ecology at the new Ship Canal deposit ground, Frodsham marshes, Cheshire. *Merseyside Nat. Ass, Bird Rep.* **1952–53**, 34–37.

Discursive notes on the birds of the settling tanks into which the dredgings from the Manchester Ship Canal are pumped, with some counts of ducks.

Andrew, D. G. & Sandeman, G. L. (1953). Notes on the birds of the Flannan Isles. *Scot. Nat.* **65**, 157–166.

An annotated list of twenty-three species which have at some time or other been recorded as breeding in these remote Outer Hebridean islands. In the past seventy years two species have been added to the breeding list (starling, fulmar), three species have probably and three more certainly ceased to breed, while two further species which do not now breed may in fact never have done so.

Bagenal, T. B. & Millar, R. H. (1954). A list of the birds of the Great Cumbrae. *Glasgow & W. Scot. Bird Bull.* **3**, 33–36.

The birds of an island in the Firth of Clyde.

Baynes, E. S. A. (1954). Report on migrant insects in Ireland for 1953. *Irish Nat. J.* **11**, 195–197.

The year was a poor one for migrant insects, only three species of butterfly, seven of moth, and one dipteran occurred. The fly was *Coelopa frigida* on Tory Island, in the same year that it was a pest on the south coast of England.

Benham, E. (1953). The distribution of squirrels in Dorset, 1945–1951. *Proc. Dorset Nat. Hist. Fld Cl.* **74**, 121–132.

Results of a parish-by-parish survey of the distribution of the red and grey squirrels in Dorset. Between 1945 and 1951 the status of the two species was reversed, the red decreasing and the grey increasing, but there is no evidence of the grey having driven out the red, which appears to have declined independently of the advance of the grey.

Benson, R. B. (1953). Some changes and additions to the list of British sawflies with the descriptions of two new species (Hym. Tenthredinidae). *Ent. Mon. Mag.* **89**, 150–154.

Also includes two species recorded from Britain for the first time.

Benson, R. B. (1953). The sawfly *Tenthredo temula* of British authors is an undescribed species (Hym., Tenthredinidae). *Ent. Mon. Mag.* **89**, 275–277.

Described from adults of both sexes as *Tenthredo celtica*. The distribution in the British Isles is summarized.

Benson, R. B. (1954). Another new sawfly (Hym., Tenthredinidae) on larch in Britain. *Ent. Mon. Mag.* **90**, 113–114.

Pristiphora glauca is described from adults from Hereford. It also occurs in Buckinghamshire. Brief notes on the bionomics and diagnostic characters are included.

Benson, R. B. (1954). The larva of the sawfly *Pristiphora retusa* (C. G. Thomson) (Hym., Tenthredinidae). *Ent. Mon. Mag.* **90**, 92.

The occurrence of this species in Inverness-shire constitutes a new record for Britain. The larva is described for the first time.

Boase, H. (1951). Sheld-duck on the Tay Estuary. *Brit. Birds*, **44**, 73–83.

Counts of *Tadorna tadorna* were made in the upper Tay Estuary from 1934 to 1950, and fluctuations in the breeding population are discussed. Data for brood size, fledging periods, and the formation of juvenile packs are given. It is suggested that the development of the frontal knob, which is delayed or absent in many males, may mark those that will breed; and that moult may be delayed in 'caretaker' birds.

Boyd, J. M. (1954). The St Kilda Wren in village area, Hirta, 1952. *Scot. Nat.* **66**, 47–49.

Twelve or thirteen pairs were counted, approximately the same number as in 1938 and 1939 in the same area.

Brady, F. (1951). Common Scoters on the North Northumberland Coast. *Brit. Birds*, **44**, 413–414.

The results of six years observations on a stretch of rocky shore. Seasonal changesi n the proportion of ages and sexes were noted.

Britten, H. (1954). Records of some of the rarer Trypetidae. *Ent. Rec.* **66**, 156–157.

Includes four new records for Surrey, one of which is for *Acanthiophilus helianthi* hitherto regarded as a coastal species, breeding for the first time in the British Isles, and also several records from Gloucestershire, Sussex and Scotland.

Brown, E. S. (1954). Report on the Corixidae (Hemiptera) taken in light-traps at Rothamsted Experimental Station. *Proc. R. Ent. Soc. Lond.* (A) **29**, 17–22.

An account of the Corixidae taken in light traps during the years 1946–1950. The use, in 1950, of a Robinson light trap with mercury vapour lighting during the time of the autumn migration resulted in high catches. The catches are analysed and comparisons are made with previous observations on spring migrations.

Brown, R. H. (1954). The warblers. *Trans. Carlisle Nat. Hist. Soc.* **8**, 23–32.

Notes on the habitat and breeding biology of nine species of warbler that breed in some part or other of the Lake District—all the British breeding species except the reed, marsh and Dartford warblers.

Brown, S. C. S. (1953). The Stigmellidae (Lep.) of the Bournemouth district. *Ent. Mon. Mag.* **89**, 158–160.

This list, with food plants, abundance and, in some cases, localities, includes seven new records from Dorset and five from Hampshire.

Browning, E. (1954). The accidental importation of three species of *Torania* into Great Britain, with observations of live specimens (Araneae: Sparassidae). *Proc. Zool. Soc. Lond.* **124**, 213–217.

Bryson, D. K. (1954). Carmarthenshire Heronries. *Ann. Rep. West Wales Fld. Soc.* **6**, 22–23.

A census in 1949 showed seven certain heronries with a population of about 42 pairs. Additional particulars are given up to 1953.

Bull, A. J. (1953). The wildfowl and waders of Poole Harbour. *Proc. Dorset Nat. Hist. Fld Cl.* **74**, 149–170.

Includes a brief account of the recent history of Poole Harbour, discussing the disappearance of *Zostera marina* by early 1930's and colonization by *Spartina townsendii* since 1907. There follows an assessment, from records of the Dorset Field Ornithology Group during the three winters between 1949 and 1952, of the status in the region of twenty-three ducks and geese and twenty-waders. Detailed consideration is given to habitat selection by turnstone, ringed plover and bar- and black-tailed godwit.

Cadman, W. A. (1954). The status of Geese in Wales. *Ann. Rep. West Wales Fld. Soc.* **16**, 18–20.

Species which regularly winter in Wales are the common white-fronted, the Greenland white-fronted, the grey lag and pink-footed. Bean, brent and barnacle geese are occasional visitors. Canada geese are resident in parts of eastern Wales. The red-breasted goose has been recorded.

Carlisle, D. B. (1954). *Styela mammiculata* n.sp., a new species of ascidian from the Plymouth area. *J. Mar. Biol. Ass. U.K.* **33**, 329–334.

Description based on four specimens collected in the Plymouth area in 1953.

Carlisle, D. B. & Carlisle, A. I. (1954). Notes on the Didemnidae (Ascidiacea). I. The presence of *Didemnum* (*Leptoclinides*) *faerōense* (Bjerkan) in the Plymouth area. *J. Mar. Biol. Ass. U.K.* **33**, 21–25.

Records presence of this species, not previously found in the British Isles.

Cawkell, E. M. (1950). Sex ratio of Common Scoter off part of the coast of S.E. England. *Brit. Birds*, **43**, 304–305.

Observations in the Dungeness-Hastings area show that males frequently preponderate. Results of a number of counts between 1938 and 1947 are recorded.

Clark, D. J. (1954). *Cistogaster globosa* Fabricius (Diptera, Tachinidae) new to Britain. *Entomologist*, **87**, 53.

A note of its occurrence in South Hampshire.

Cloudsley-Thompson, J. L. (1953). Notes on Arachnida, 19.—Biological observations, etc. *Ent. Mon. Mag.* **89**, 88–89.

Hyctia nivoyi recorded for the first time from Surrey.

Collingwood, C. A. (1954). Ants (Hym., Formicidae) in Berwickshire. *Ent. Mon. Mag.* **90**, 23.

Includes five new county records.

Collingwood, C. A. (1954). The ants (Hym., Formicidae) of a country garden. *Ent. Mon. Mag.* **90**, 43.

Includes new records for Worcestershire, Hereford and Warwickshire.

Collingwood, C. A. (1954). Rare ants (Hym., Formicidae) in Dorset. *Ent. Mon. Mag.* **90**, 43–44.

Includes the first record for *Anergates atratulus* outside Hampshire.

Colyer, C. N. (1954). A new species of *Megaselia* (Dipt., Phoridae) from Britain: notes on British fungicolous Phoridae. *Ent. Mon. Mag.* **90**, 108–112.

M. buxtoni, described from adults bred from *Pleurotus cornucopiae* in Buckinghamshire. Includes records of other Phorids bred from fungi, with the species attacked and localities, and a list of the British species known to breed regularly or occasionally in fungi.

Conder, P. J. (1953). A list of the birds of Skokholm, Pembrokeshire. *Northw. Nat.* (N.S.) **1**, 211–219.

Information on numbers and status, based almost entirely on summer records.

Coombes, R. A. H. (1950). The moult migration of the Sheld-duck. *Ibis*, **92**, 405–418.

Observations made in Morecambe Bay led to the discovery that *Tadorna tadorna* migrates overland in July to concentrate in the Heligoland Bight for the moult. The return is very gradual, being spread over six months.

Cowley, J. (1953). Odonata from Gloucestershire and Glamorgan. *Ent. Mon. Mag.* **89**, 139–140.

Records for the Forest of Dean, the Gower peninsular, and Kenfig Burrows, including the first for *Ischnura pumilio* from Wales.

Cribb, J. (1954). The species of *Plateumaris* and *Donacia* (Col., Chrysomalidae) in Sussex. *Ent. Mon. Mag.* **90**, 80.

Habitats, localities and abundance for all the British *Plateumaris* and all but two of the British *Donacia*.

d'Assis-Fonseca, E. C. M. & Cowley, J. (1953). Insects and spiders collected in Glamorgan, June and July, 1952. *Trans. Cardiff Nat. Soc.* **81**, 66–74.

Forty-six species of Hymenoptera, 252 Diptera, and smaller numbers of other insect Orders collected in coastal regions of the county.

Day, F. H. (1954). Notes on Cumberland beetles. The genus *Philonthus* Steph. *Northw. Nat.* (N.S.) **2**, 226–228.

Localities, habitats and numbers for thirty-four species.

Day, F. H. (1954). *Dacne bipustulata* (Thunb.) (=*humeralis* (F.)) (Col., Erotylidae) in Cumberland. *Ent. Mon. Mag.* **90**, 134.

On *Polyphorus* [*sic*] *squamosus* in Cumberland. A new county record.

Doncaster, J. P. (1954). Two Aphids new to Britain. *Entomologist*, **87**, 127–128.

Periphyllus californiensis on *Acer palmatum* and *A. japonica* in Surrey and *Aphis verbasci* on *Verbascum phlomoides* in Essex.

Eastop, V. F. (1953). A list of aphids collected in Guernsey, Herm and Sark. *Ent. Mon. Mag.* **89**, 154–155.

With food plants and localities.

Edmondson, T. (1953). Some aspects of the natural history of Western Chat Moss. Birds, mammals and selected flowering plants. *Northw. Nat.* (N.S.) **1**, 400–416.

Includes a list of birds, showing abundance, status, habitats and seasonal data, and one of mammals, showing abundance and habitats, with information on the main vegetation areas.

Edmonson, T. (1953). The spring migration of wagtails and hirundines in south-east Lancashire. *Northw. Nat.* (N.S.) **1**, 558–562.

The results of counts of hirundines, swifts, yellow and white wagtails, wheatear and meadow pipit between mid-April and mid-May in 1951 and 1952 at two flooded colliery subsidences are given and discussed. Movements of yellow and white wagtails were similar in April, but the latter usually continued for one or two weeks in May. Waves of hirundines coincided with waves of yellow wagtails during the latter half of April, but continued until mid-May. Some evidence was obtained that the passage of meadow-pipits coincided with that of yellow wagtails. The main movement of swifts occurred about a fortnight later than that of hirundines, and their wave patterns bore little resemblance. Factors affecting wave-pattern in crossing Britain are discussed; aggregations of birds during adverse weather at favoured feeding grounds or sheltered halting places are best regarded as continually absorbing and emitting streams or series of small waves.

Edmonson, T. (1954). The birds of the south-east Lancashire Flashes. *Northw. Nat.* (N.S.) **2**, 57–78.

A correlation of published and unpublished records of birds at Leigh (Pennington) Flash over some 30 years, with dates, numbers and information on status. The average arrival dates of twelve migrants are given in an appendix, which also contains histograms showing for ten passage migrants the number of occurrences, or total number of birds, per month throughout the year.

Ellison, N. F. (1954). Notes on the marine fishes of Cheshire and Liverpool Bay. *Northw. Nat.* (N.S.) **2**, 49–56.

Notes on the occurrence of 34 species.

Emmet, A. M. (1954). *Nonagria algae* Esper (cannae Ochs.) (Lep., Caradrinidae) in Ireland. *Entomologist*, **87**, 31.

This record, from Co. Galway, is the first from Ireland. The nearest English station is some 400 miles distant in the south-east.

Evans, G. O. (1954). Some new and rare species of Acarina. *Proc. Zool. Soc. Lond.* **123**, 793–811.

Important British records.

England, M. D. (1951). Large roost of Bramblings. *Brit. Birds*, **44**, 386.

The roost in two acres of woodland in Kent was occupied by several thousand *Fringilla montifringilla* for at least a month, in rhododendrons under tall oaks.

Fidler, J. H. (1953). The biology of some Yorkshire Aphides, III. *Northw. Nat.* (N.S.) **1**, 220–226.

Brief notes on the food plants, abundance and life-cycles of twenty-six additional species, with localities and dates. Rather more than one hundred aphids have now been noted in Yorkshire. Corrections to the identity of three species previously recorded [*Northw. Nat.* **22**, 242–248 (*J. anim. Ecol.* **18**, 234); **23**, 105–112 (*J. anim. Ecol.* **22**, 183)] are included.

Fitter, R. S. R. (1954). Late autumn migration from Pembrokeshire to Ireland. *Fair Isle Bird Obs. Bull.* **2**, 93–96.

Draws attention to an apparently little known movement, mainly of starlings, from Pembrokeshire to Ireland in the first half of November.

Ford, W. K. (1953). Lancashire and Cheshire Odonata. (A preliminary list.) *Northw. Nat.* (N.S.) **1**, 227–233.

A list, based on the literature and records by local observers, of some twenty species from Lancashire and twenty-three from Cheshire, with localities, dates and notes on abundance.

Fraser, J. H. (1954). Warm-water species in the plankton off the English Channel entrance. *J. Mar. Biol. Ass. U.K.* **33**, 345–346.

Occurrence of the tropical salps *Ritteriella picteti* and *R. amboinensis* and the large tropical diatom *Ethmodiscus gazellae* off the English Channel.

French, R. A. (1953). Insect migration records, 1952. *Entomologist*, **86**, 157–164.

Summary of migratory movements recorded in 1952.

Galliford, A. L. (1953). Notes on the distribution and ecology of the Rotifera and Cladocera of North Wales. *Northw. Nat.* **24**, 513–529.

An annotated list of species including a station list and some introductory notes on the localities.

Galliford, A. L. (1954). Notes on the freshwater organisms of Lundy with especial reference to the Crustacea and Rotifera. *7th Ann. Rep. Lundy Fld Soc.* **1953**, 29–35.

The fauna of eighteen ponds and pools and one stream on an island in the Bristol Channel, mainly isopods, copepods, cladocerans and rotifers. It is suggested that some may have been introduced with fish in the past.

George, R. S. (1953). *Euophryum confine* Broun (Col., Curculiondae [*sic*]) in Gloucestershire East and Essex. *Ent. Mon. Mag.* **89**, 155.

A new record for Gloucestershire.

Gibson, J. A. (1954). Bird notes from Ailsa Craig, 1953. *Glasgow & W. Scot. Bird Bull.* **3**, 3–6.

Estimates of numbers of breeding birds on this well-known small island in the Firth of Clyde.

Gibson, J. A. (1954). Bird notes from Holy Island, Arran. *Glasgow & W. Scot. Bird Bull.* **3**, 38–41.

A list of the breeding birds based on eight visits since 1944.

Gibson, J. A. & Gordon, C. J. (1953). The breeding birds of Inchmarnock. *Glasgow & W. Scot. Bird Bull.* **2**, 54–57.

Short notes on the breeding species of a small island in the Sound of Bute, with estimates of the population of many of them. Fifty-six species bred in 1953.

Gordon, S. (1954). The bird life of Tuilm Island, Skye. Changes in the last twenty-five years. *Glasgow & W. Scot. Bird Bull.* **3**, 2–3.

Decreases in the population of certain sea-birds are attributed to oil pollution.

Green, J. (1953). Observations on *Hypogastrura viatica* sensu Stach, 1949, and other Collembola in Carmarthenshire. *Ent. Mon. Mag.* **89**, 289–291.

Contains the first species list for the county, based on collections in April 1952. *Hypogastrura viatica* was abundant on firm, damp sand and on a pool in December, but was not present in April or August. The individuals on the pool were considerably larger than the others.

Grey, F. G. (1950). Non-breeding Fulmars. *Brit. Birds*, **43**, 305.

Observations at Marsden, Co. Durham, in 1949 which support the view that more than half the birds present in a colony may not be breeding.

Griffin, D. E. (1953). A species of *Tetrix* Latreille new to Jersey, Channel Islands (Orth., Tetrigidae). *Ent. Mon. Mag.* **89**, 198.

Tetrix vittata. The record for *T. ceperoi* is confirmed.

Hardy, A. C. & Bainbridge, R. (1954). Experimental observations on the vertical migrations of plankton animals. *J. Mar. Biol. Ass. U.K.* **33**, 409–448.

By using a circular Perspex tube filled with sea water and mounted so that it can be rotated in a vertical plane, the vertical migrations of planktonic animals may be recorded. Vertical migrations appear to be predominantly direct up-and-down swimming with only a few small forms moving in an indirect manner. Downward migration is an active swimming movement, not a passive sinking. The speeds of vertical swimming of various animals are recorded. Vertical migration is greatly influenced by light intensity.

Harrison, J. W. Heslop- (1954). Lepidoptera from the Outer Hebrides in 1953. *Entomologist*, **87**, 83–86.

An annotated list of species found in Lewis, Harris, Killegray, Taransay, Shillay and Coppay, including a new record from the Outer Hebrides and one for Harris.

Harwood, N. (1954). Bird notes from the Fylde Coast. *Northw. Nat.* (N.S.) **2**, 184–190.

Records for some 170 species observed over a period of four years, with observations on the distribution of gulls and waders on sand and mud beaches and on marshland.

Hewson, R. (1950). Corn-Bunting roost in Moray. *Brit. Birds*, **43**, 370.

About 150 roosted in rush tussocks below a power line on which they had assembled in late December, but there were none in the area a week later.

Hickin, N. E. (1953). *Neuronia ruficrus* Scopoli (Trich., Phryganeidae) in Sussex. *Ent. Mon. Mag.* **89**, 168.

A new record for south-east England.

Hollom, P. A. D. (1951). Great Crested Grebe sample census: report to end of 1950. *Brit. Birds*, **44**, 361–369.

The survey covers twenty-one English counties for the five years 1946–1950. There is considerable local fluctuation in the population of *Podiceps cristatus*, but over the whole area it is remarkably constant, 1947 being the only year when the total population declined greatly, and recovery in 1948 brought it back to normal.

Homes, R. C. (1953). The duck census in the London area 1951–1953. *Lond. Bird Rep.* **17**, 38–41.

The population trends for each of nine species during the winters of 1951–52 and 1952–53 are briefly discussed with some reference to weather and to numbers noted in previous years. Mallard, wigeon and pochard all declined, whereas teal and smew became more numerous.

Ingram, G. C. S. & Salmon, H. M. (1953). Ornithological notes 1950–52. *Trans. Cardiff Nat. Soc.* **81**, 93–97.

Notes on seventy-two species from Glamorgan and thirty-two species from Monmouthshire.

Jackson, D. J. (1954). Notes on water beetles from the island of Raasay. *Scot. Nat.* **66**, 30–34.

A list of twenty-eight species, with their habitats.

Jeannel, R. (1954). Un Psélaphide nouveau des Iles Britanniques. *Ent. Mon. Mag.* **90**, 106.

Euplectoides pearcei gen. et sp.n. described from a male taken in a wood in Herefordshire.

Johnston, T. L. (1954). The greater black-backed gull on the Cumberland Solway. *Trans. Carlisle Nat. Hist. Soc.* **8**, 8–13.

Notes on population trends, food, and breeding and winter habits.

Kevan, D. K. McE. (1952). A summary of the recorded distribution of British Orthopteroids. *Trans. Soc. Brit. Ent.* **11**, 165–180.

A useful summary of vice-comital records for British species of Dictyoptera, Embioptera, Phasmatodea, Orthoptera and Dermaptera.

Kevan, D. K. McE. (1953). Notes on the distribution of British Orthopteroids. *J. Soc. Brit. Ent.* **4**, 119–122.

Additions and corrections to the paper published in 1952, *Trans. Soc. Brit. Ent.* **11**, 165–180.

Kimmins, D. E. (1954). *Caenis robusta* Eaton, a species of Ephemeroptera new to Britain. *Ent. Mon. Mag.* **90**, 117–118.

Recorded from Norfolk. Includes a description of the adults and diagnostic characters.

Kitchen, T. B. (1954). *Perigona nigriceps* Dejean (Col., Carabidae) in Windsor Forest. *Ent. Mon. Mag.* **90**, 71.

A new county record and the second for the British Isles.

Lancaster, D. G. (1953). A check list of the mammals of Northern Rhodesia. *Lusaka: Govt. Printer*, vii + 56 pp. (4*s.*).

A taxonomic list including over 260 mammals, with general notes on their distribution and broad ecological requirements.

LeQuesne, W. J. (1954). *Tetrix subulata* (L.) (Tetrigidae), an addition to the Orthoptera of Jersey, Channel Islands. *Ent. Mon. Mag.* **90**, 20.

Lever, R. J. A. W. (1954). The mosquito *Culex torrentium* Mar. (Dipt., Culicidae) new to Dorset. *Ent. Mon. Mag.* **90**, 65.

Lloyd, R. W. (1953). *Ostoma ferrugineum* L. (Col., Clavicornia, Ostomidae) new to Britain. *Ent. Mon. Mag.* **89**, 251.

Under bark of Scots pine in Aberdeenshire. Includes a description of the adult.

Lockley, R. M. & Marchant, S. (1951). A midsummer visit to Rockall. *Brit. Birds*, **44**, 373–383.

Includes field notes on *Fulmarus glacialis* with special reference to their dependence on trawlers; the connexion between the development of the deep-sea fishing industry and the great increase and spread of *F. glacialis* in recent years is discussed.

Longfield, C. (1954). The British dragonflies (Odonata) in 1952 and 1953. *Entomologist*, **87**, 87–91.

Includes a record of *Aeshna affinis* new to Britain, new county and breeding records and deals with some thirty-four species.

MacDonald, J. D. (1951). Kestrels at sea. *Ibis*, **93**, 308–309.

Three *Falco t. tinnunculus* remained on board a ship steaming south off the West African coast for three days, and it is suggested that the birds were aware of their geographical position, and of the direction of the ship's movement.

Macmahon, C. & Hompstead, K. E. (1954). Bird observation on Rathlin Island. *Irish Nat. J.* **11**, 192–195.

A list of the birds seen during a week in January 1954.

Massee, A. M. (1952). Notes on some interesting insects observed in 1951. *Rep. E. Malling Res. Sta.* **A. 35** (1951). 155–161.

Notes on some of the more interesting insects and mites found on fruit by growers in S.E. England. Details are given of any damage caused and suggestions made for controlling the more harmful species.

Massee, A. M. (1952). Notes on some interesting insects observed in 1952. *Rep. E. Malling Res. Sta.* **A. 36** (1952), 146–150.

Comments on some of the more interesting insects and mites found on fruit in 1952, and sent in to the research station by growers in S.E. England, with details of any damage caused and suggestions for controlling the more harmful species.

Matheson, C. (1954). The 'Wild' Goat in Wales. *Ann. Rep. West Wales Fld. Soc.* **16**, 13–16.

A brief survey of the past and present status of feral goats.

Melluish, W. D. (1952, 1953). The census of great crested grebe, 1951 [1952]. *Lond. Bird Rep.* **16**, 37–38 [**17**, 41–42].

The total number of adults in the London area declined by 6·8 % in each year, in 1951 chiefly owing to the absence of large numbers of non-breeding birds in concrete-banked reservoirs in Surrey and Essex. Numbers in Herts and Middlesex reached maxima in this year, but in 1952 they declined, in the latter county sharply owing to the filling in of some gravel pits, whereas they increased in the other four counties. In both years, the birds were most numerous on gravel pits. There appeared to be some decrease in breeding numbers in 1952.

Moore, B. P. (1953). *Arhopalus* (=*Criocephalus*) *rusticus* L. (Col., Cerambycidae) in Surrey. *Ent. Mon. Mag.* **89**, 274.

This Cerambycid, which appears to be established in Surrey, is recorded there for the first time.

Murgatroyd, J. H. (1953). Four new spider records. *Ent. Mon. Mag.* **89**, 248.

Includes a new county record for Shropshire and one for Glamorgan.

Murgatroyd, J. H. (1954). *Megabunus diadema* F. (Opiliones, Phalangiidae) in Wales. *Ent. Mon. Mag.* **90**, 18.

Recorded for the first time in Wales, from Flintshire and Merioneth.

Murgatroyd, J. H. (1954). Additional spider records. *Ent. Mon. Mag.* **90**,

New records for Dorset, Cardigan, Merioneth, Somerset and Suffolk.

Owen, J. H. (1951). The nesting of the Greater Whitethroat. *Trans. Caradoc Fld Cl.* **1945 & 1946**, 127–130.

Records local observations from 1938 to 1946 on dates, size of clutch, types of nest and nesting habits.

Paine, J. (1952). List of insects occurring on the hop. *Rep. E. Malling Res. Sta.* **A. 35** (1951), 179–180.

A guide to the frequency of their occurrence is also given.

Parmenter, L. (1953). Additions to the British list of Agromyzidae (Dipt.). *Ent. Mon. Mag.* **89**, 178–180.

Includes characters, food plants, habitats, localities and dates for eight species new to Britain, as well as two additions to the Cambridgeshire list.

Philipson, M. (1954). North-eastern bird studies. *Trans. Carlisle Nat. Hist. Soc.* **8**, 14–22.

Field notes, mainly on breeding biology, on the curlew *Numenius arquata* and the black grouse *Lyrurus tetrix* with some references to food, habitat and movements.

Phillips, W. W. A. (1950). Goldfinches at sea. *Ibis.* **92**, 477.

A midwinter record of northwards movement off the Spanish coast.

Popham, E. J. (1953). Observations on the migration of Corixids (Hem.) into a new aquatic habitat. *Ent. Mon. Mag.* **89**, 124–125.

A discussion of the results of experiments with *Corixa nigrolineata* released from the edge of quarries with and without water, in which the direction and distance flown are related to direct and reflected light.

Powell, H. T. (1954). Occurrence of *Chthamalus stellatus* (Poli) in Fair Isle and Shetland. *Nature, Lond.* **173**, 688.

Rae, B. B. & Wilson, E. (1953). Rare and exotic fishes recorded in Scotland during 1952. *Scot. Nat.* **65**, 141–153.

An annotated list of thirty species. The unusual features of the year included a heavy invasion of the North Sea by Ray's Bream *Brama raii* in the autumn; the presence of various southern fish off the east coast in the autumn; the presence of a few deep-water fishes in the northern North Sea; and the presence of the Sun Fish *Mola mola* off the west coast in the summer.

Roy, A. B. (1954). The spiders of Eigg and Mull. *Scot. Nat.* **66**, 35–37.

A list of thirty-five species, without habitats.

Ruttledge, R. E. (1954). Report on observations of birds at Irish light-stations, 1953. *Irish Nat. J.* **11**, 199–200.

Only one notable rush of migrants, on 6–9 May, was recorded. A list of the more interesting occurrences is given.

Ruttledge, R. F. & Weaving, J. (1954). Autumn migration (1953) at Great Saltee, S.E. Ireland. *Fair Isle Bird Obs. Bull.* **2**, 81–91.

Bird migration notes at the Great Saltee Bird Observatory from 12 September to 16 November.

Salmon, M. A. (1954). A new variety of *Tettigella viridis* (L.) (Cicadellide) [*sic*] and other Auchenorhyncha from central South Wales. *Entomologist*, **87**, 64–68.

Includes lists of Cercopidae, Cicadellidae, Cixiidae and Delphacidae, with numbers, habitats and localities in Merioneth, Pembrokeshire and Brecknock during August 1952 and 1953.

Scott, D. (1954). Notes on the birds of the Shiant islands. *Glasgow & W. Scot. Bird Bull.* **3**, 36–38.

The breeding birds of a group of Hebridean islands, with a brief mention of the mammals.

Smith, K. G. V. (1954). *Meconema thalassinum* (Degeer) (Orth., Tettigoniidae) in Shropshire. *Ent. Mon. Mag.* **90**, 21.

A new county record.

Smith, K. G. V. (1954). Further notes on the Lepidoptera of Shropshire. *Entomologist*, **87**, 107–111.

Records, with localities, dates and, in some cases, food plants, for sixty additional species observed in 1951–53. [See also 1952, *Entomologist* **85**, 25–32. Abstract in 1953, *J. Anim. Ecol.* **22**, 405.]

Steel, W. O. (1953). A species of *Carpelimus* (Col., Staphylinidae) new to Britain. *Ent. Mon. Mag.* **89**, 214.

C. obesus on mud on the bank of a stream in Berkshire. Includes a description of the adult.

Stelfox, A. W. (1953). *Perilitus borealis* Thomson (Hym., Braconidae) in Ireland and new to the British Isles. *Ent. Mon. Mag.* **89**, 141.

Stelfox, A. W. (1953). A new *Rogas* (Hym., Braconidae) from Ireland. *Ent. Mon. Mag.* **89**, 146–147.

Description of *R. heterostigma* from Queen's County and Co. Kildare, with diagnostic characters.

Tozer, D. (1953). *Pogonochaerus fasciculatus* Deg. (Col., Lamiidae) breeding in England. *Ent. Mon. Mag.* **89**, 170.

A new county record for Norfolk.

Venables, L. S. V. & Venables, U. M. (1950). The Corn-Crake on Shetland. *Brit. Birds*, **43**, 137–141.

A decline in numbers is attributed to preference for rye-grass for nesting, early mowing resulting in the loss of many nests.

Wadley, N. J. P. (1952). Black redstarts in the London area, 1951. *Lond. Bird Rep.* **17**, 32–34.

Breeding, non-breeding and winter records for *Phoenicurus ochrurus* in the City are summarized and some additional records for Outer London in previous years given. The number of breeding pairs fell to nine, probably owing to the failure of young birds of the previous year to return, and fifteen broods were produced, of which thirteen survived. In general, rebuilding operations did not interfere with breeding.

Williamson, K. (1951). The wrens of Fair Isle. *Ibis*, **93**, 599–601.

A new race *Troglodytes troglodytes fridariensis* is described, and the population is estimated at 30 to 40 pairs, all nesting on the coast. It is pointed out that island wrens are so sedentary that the distinctness of the Fair Isle and Shetland stocks is proof of their long isolation, though separated by only 25 miles of sea.

Williamson, K. (1953). A week of wheatear passage. *Fair Isle Bird Obs. Bull.* **2**, 35–37.

Correlation of arrivals of *Oenanthe oenanthe* at Fair Isle with the weather conditions in the north Atlantic between the British Isles, Greenland and Iceland.

Williamson, K. (1954). American birds in Scotland in autumn and winter, 1953–54. *Scot. Nat.* **66**, 13–29.

Notes on the occurrence of *Anser caerulescens*, *Histrionicus histrionicus*, *Coccyzus americanus*, *C. erythrophthalamus*, *Hylocichla minima* and *Calcarius lapponicus*, with a discussion of the meteorological conditions over the Atlantic which make it probable that these were genuine transatlantic migrants.

Williamson, K. & Davis, P. (1954). The phenomenal invasion of Lapland buntings in September 1953. *Fair Isle Bird Obs. Bull.* **2**, 51–55.

Relates the incursion to weather conditions over the North Atlantic.

Williamson, M. H. (1953). *Dilta hibernica* (Carp.) (Thysanura, Machilidae) in Oxfordshire and Yorkshire. *Ent. Mon. Mag.* **89**, 288.

A first record for Oxfordshire.

Wilson, N. H. (1951). Hybrid Glaucous × Great Black-backed Gull at Limerick. *Brit. Birds*, **44**, 286–287.

A description is given of a natural hybrid, the description agreeing with that of two produced in captivity.

Winterbottom, R. H. (1954). A winter census of gulls. *Starfish*, **7**, 9–14.

Counts of four species of gull on the playing fields of Dulwich College, South London, during the winters of 1951–52 and 1952–53, with notes on meteorological and other factors affecting the fluctuations in numbers.

Wolff, T. (1954). Occurrence of two East American species of crabs in European waters. *Nature, Lond.* **174**, 188–189.

On recent evidence from continental waters it is suggested that *Callinectes sapidus* and *Rhithropanopeus harrisi* may occur around British shores.

Wood-Baker, C. S. (1953). Records of forty-two European aphids (Hem.). *Ent. Mon. Mag.* **89**, 68–70.

Includes many records, with dates, localities, habitats and life forms, for British species of fifteen genera.

Wood-Baker, C. S. (1953). Records of seventy European aphids (Hem.). *Ent. Mon. Mag.* **89**, 108–113.

Includes records, with dates, localities, habitats and life forms, for British species of ten genera.

Wood-Baker, C. S. (1953). Records of twenty European aphids (Hem.). *Ent. Mon. Mag.* **89**, 176–177.

Includes records, with dates, localities, habitats and life forms, for British species of eight genera.

Wood-Baker, C. S. (1953). Records of forty-six European aphids (Hem.). *Ent. Mon. Mag.* **89**, 265–270.

Includes records, with dates, localities, habitats and life forms, for British species of twenty genera.

Wood-Baker, C. S. (1954). Records of European aphids (Hem.). *Ent. Mon. Mag.* **90**, 149–153.

Includes localities, dates and food plants for species of eight British genera.

Woodcock, A. J. A. (1954). The aquatic Coleoptera of North and South Northumberland, *Ent. Mon. Mag.* **90**, 25–31.

Contains a list of the recorded species, with a short topographical account.

Wynne-Edwards, V. C. (1953). Leach's petrels stranded in Scotland in October-November, 1952. *Scot. Nat.* **65**, 167–189.

A detailed account of the great 'wreck' of *Oceanodroma leucorhoa* in the autumn of 1952, in so far as it affected Scotland. An uninterrupted series of westerly gales in the North Atlantic is held to have been responsible. Appendices give precise details of over 500 Leach's and stormy petrels picked up in Scotland that autumn.

Yarrow, I. H. H. (1954). Records of Aculeate Hymenoptera at Hampstead. *Entomologist*, **87**, 168–169.

Some additions and amendments to a previous account [See 1948, *Lond. Nat.* **27** (1947), 81–111. Abstract in 1949, *J. Anim. Ecol.* **18**, 234.]

6. STUDIES ON BEHAVIOUR

Alley, R. & Boyd, H. (1950). Parent-young recognition in the Coot *Fulica atra*. *Ibis*, **92**, 46–51.

Based on forty or fifty incidents observed in two seasons at Blagdon reservoir, Somerset.

Armstrong, E. A. (1950). The significance of the dark ventral plumage of wading birds breeding in high latitudes. *Ibis*, **92**, 480–481.

A note giving instances among passerines of open, homogeneous, terrestrial habitats, and suggesting the significance is ecological rather than geographical.

Armstrong, E. (1951). Discharge of oily fluid by young Fulmars. (A supplementary note to 'Field studies on the Fulmar', by Eric Duffey). *Ibis*, **93**, 245–251.

The squirting of oil by young *Fulmarus glacialis* is attributed to be primarily a defence against winged predators, and to have enabled the species to extend its range from the Antarctic to the North Atlantic.

Armstrong, E. A. (1951). The significance of a dark ventral surface in certain birds. *Ibis*, **93**, 314–315.

A reply to Meinertzhagen's note (1951, *Ibis*, **93**, 140) on this subject, affirming that none of the instances given refute the theory that dark underparts are correlated with display behaviour.

Ash, J. (1950). Intruder responses in birds outside their breeding areas. *Brit. Birds*, **43**, 54–55.

Examples are given for *Sterna dougallii*, *Tringa totanus*, and *Larus ridibundus*. The behaviour is not confined to the breeding season, but appears to occur only in a habitat suitable for breeding.

Badcock, R. M. (1953). Observations of oviposition under water of the aerial insect *Hydropsyche angustipennis* (Curtis) (Trichoptera). *Hydrobiologia*, **5**, 222–225.

Describes behaviour of the female caddis fly observed in the laboratory to enter water and oviposit, and discusses briefly the ecological implications of the actions observed.

Blair, H. M. S. (1950). Rodent-run distraction-behaviour in birds. *Ibis*, **92**, 476.

A note recording instances in seven species of waders, and in two races of *Motacilla flava*.

Blair, H. M. S., Oliver, H. R., Chisholm, A. H. (1950). Rodent-run distraction-behaviour in birds. *Ibis*, **92**, 476–477.

Cites instances in *Actitis hypoleucos* and in several Australian genera.

Brown, R. H. J. (1951). Flapping flight. *Ibis*, **93**, 333–359.

A comprehensive study of bird flight which includes an illustrated account of the wing movements of a pigeon based on cinematograph records.

Butler, C. G. (1954). The method and importance of the recognition by a colony of honey-bees (*A. mellifera*) of the presence of its queen. *Trans. R. Ent. Soc. Lond.* **105**, 11–29.

Extensive experiments show that worker bees of a colony inform each other of the presence of their queen through the medium of 'queen substance'. The nature and origin of this substance is discussed. It is suggested that this is the most important single factor in the maintenance of colony cohesion.

Cloudsley-Thompson, J. L. (1952). Studies in diurnal rhythms: II. Change in the physiological responses of the woodlouse *Oniscus asellus* to environmental stimuli. *J. Exp. Biol.* **28**, 295–303.

A diurnal locomotory rhythm, partly endogenous and primarily controlled by light and darkness is demonstrated. The interrelations of humidity, carbon dioxide, light and recent history of the animal are considered and these results are related to the behaviour of the woodlouse in nature.

Cassera, J. (1951). Display-flight of Spotted Flycatcher. *Brit. Birds*, **44**, 409.

Davis, T. A. W. (1951). Distraction-display of Common Partridge. *Brit. Birds*, **44**, 209.

An instance of the 'rodent run' type of distraction display, with no suggestion of 'injury-feigning'.

Duffey, E., Creasey, N. & Williamson, K. (1950). The 'rodent-run' distraction-behaviour of certain waders. *Ibis*, **92**, 27–33.

Distraction-display of *Calidris maritima* is described, the origin of such displays is discussed, and eight other species in which the 'rodent-run' occurs are listed with references.

Dunnett, G. E. & Hinde, R. A. (1953). The winter roosting and awakening behaviour of captive great tits. *Brit. J. Anim. Behaviour*, **1**, 91–95.

Observations on winter behaviour of great tits in an aviary, and discussion of the implications of this behaviour relative to the bird's diurnal rhythm, weather, feeding, sexual condition and the like.

George, W. (1953). Some animal reactions to variations of temperature. *Endeavour*, **12**, 101–105.

Reviews observations in which temperature appears to play a decisive role.

Gillham, E. H. (1951). Down-stripping by Sheld-Duck away from nest-site. *Brit. Birds*, **44**, 103–104.

Varying amounts of down were observed in marshes and saltings of north Kent during two seasons, most often where *Tadorna tadorna* were constantly seen. As none were found before 27 May, it is tentatively suggested that non-breeding birds may be responsible.

Goodwin, D. (1951). Some aspects of the behaviour of the Jay *Garrulus glandarius*. *Ibis*, **93**, 414–442, 602–625.

Observations on wild and captive *Garrulus glandarius* for a period of over four years. Displays, call-notes, aspects of the breeding cycle, reactions to enemies, dominance, and intra-specific aggressive behaviour are described and discussed. Acorns are probably the largest single item in the diet of adults, which spend much time burying them, and sometimes remember the hiding place. 'Anting' is described, also play, which reproduces escape tactics from an attack by an *Accipiter*.

Griffin, D. G. (1952). Bird navigation [with an appendix by Ernst Mayr on 'German experiments on the orientation of migrating birds']. *Biol. Rev.* **27**, 359–400.

Theories based on Coriolis effect, earth's magnetic field and perception of infra-red radiations are discounted and a theory of a combination of random searching with the recognition of familiar landmarks is shown to account for the observed facts. An appendix reports evidence for orientation based on the sun's position and a further appendix describes experiments in which homing birds, transferred laterally across Europe during the migration period, continued to travel along a route parallel to the original one.

Harrison, J. M. (1951). Tawny Owls found drowned. *Brit. Birds*, **44**, 100.

It is suggested that the cause of *Strix aluco* being sometimes found drowned may be their fondness of bathing, as evinced by two captive birds. One of these first uttered song only at 3 years and 4 months old.

Hunter, R. F. (1954). Some notes on the behaviour of hill sheep. *Brit. J. Anim. Behav.* **2**, 75–78.

Records observations of Scottish blackface breeding ewes on a border hill farm at between 950 and 1250 ft. The animals know their pasture, and their movements are related to the distribution of the best grazing and to the weather conditions at different seasons of the year. Periods of rest are related to sun-up and sun-down, being longer during summer days than in winter.

Kalmus, H. (1954). Sun navigation by animals. *Nature, Lond.* **173**, 657–658.

Recent work is reviewed in the light of past research.

Kalmus, H. (1954). The clustering of honeybees at a food source. *Brit. J. Anim. Behav.* **2**, 63–71.

Describes and discusses artificially induced clustering of hive bees by training them at a feeding site and then removal of food from this site,. Concludes that clustering is a 'social activity', the bees being influenced by visual and olfactory stimuli, to which may also be added mechanical vibrations.

Male, A. E. (1950). Tawny Owls found drowned. *Brit. Birds*, **43**, 157.

Two instances are given.

Meinertzhagen, R. (1951). The significance of a dark ventral surface in certain birds. *Ibis*, **93**, 140–141.

It is pointed out that a dark ventral surface is not confined to certain wading birds breeding in high latitudes, but is found in many different groups, and in various habitats, and examples show that no single explanation of its purpose can be given.

Mountfort, G. R. (1950). Blue Tit's display flights and behaviour during nest-building period. *Brit. Birds*, **43**, 186–187.

Describes a day's nest-building spread over five hours, and the behaviour and displays of the accompanying male.

Nelson, J. B. (1950). Roosting behaviour of Linnet and Chaffinch. *Brit. Birds*, **43**, 293.

Flocks seen flying round and round over thick rhododendrons before dropping down to roost.

Owen, J. H. (1951). The flights of the Red-backed Shrike. *Brit. Birds*, **44**, 166–170.

The flight in different circumstances—catching prey, seeking a mate, attacking an enemy—is described; other aspects of behaviour are also included.

Rand, A. L. (1954). Social feeding behaviour of birds. *Fieldiana, Zool.* **36**, 1–71.

Reviews the literature relating to social feeding habits of birds outside the breeding season, and discusses the advantages and disadvantages associated with the phenomenon. Both intra- and inter-specific groups are considered, as also relations with other animals than birds. It is concluded that protection from predation is of low importance, the main advantages being, in the organized intra-specific flock, reduction of competition by spacing out, guidance to food, communal flushing of prey into the open and combining of individuals in killing and securing food. Inter-specific associations benefit birds through beating activities, provision of scraps, parasites and even flesh, also through pilfering and robbing of one species by another. The possible origins of the associations and the relation to bird psychology are discussed.

Ryves, B. H., Coulson, J. C., & Congreve, W. M. (1950). Tawny Owls found drowned. *Brit. Birds*, **43**, 338–339.

Scott, H. (1953). Discrimination of colours by *Bombylius* (Dipt., Bombyliidae). *Ent. Mon. Mag.* **89**, 259–260.

Bombylius major consistently visited flowers of which the colour was purple or shades of pink or blue that included some purple. Flowers of other colours, including clear blue, were ignored.

Simmons, K. E. L. (1951). Interspecific territorialism. *Ibis*, **93**, 407–413.

Examples of interspecific territorialism are given between five species of *Oenanthe*, two *Lanius*, and between an *Erithacus rubecola* and a pair of *Saxicola torquata*. Common outline and mannerisms seem to be more important than plumage in stimulating competition. It is apparently a means by which the effect of competition between closely allied species with similar ecology is avoided.

Suffern, C. (1951). Sky-larks making 'forms'. *Brit. Birds*, **44**, 387–388.

An apparently quite common, but overlooked habit. Males, on descending after singing, make forms in tufts.

Taylor, L. R. & Kalmus, H. (1954). Dawn and dusk flights of *Drosophila subobscura* Collin. *Nature, Lond.* **174**, 221–222.

The use of suction traps at Rothamsted shows, for this species, two peaks of activity in 24 h. It is suggested from this and laboratory observations that *Drosophila* may have become adapted to increasing daytime aridity by increased visual efficiency at low light intensities together with a shift in flight periodicity to less climatically extreme, but darker times of day.

Thorpe, W. H. (1951). The learning abilities of birds. Parts 1 and 2. *Ibis*, **93**, 1–52, 252–296.

A review of what is known of the learning abilities of birds. The intimate relationship of instinct and learning as complementary aspects of the total behaviour is stressed. Definitions necessary for the full description of behaviour in all its aspects are given. References occupy eleven pages.

Thorpe, W. H. (1954). The process of song-learning in the chaffinch as studied by means of the sound spectrograph. *Nature, Lond.* **173**, 465–469.

Van Beneden, A. & Huxley, J. S. (1951). The aerial dawn chorus of the Swallow. *Brit. Birds*, **44**, 127–128.

In fine weather a song-chorus of *Hirundo rustica* occurs frequently and regularly, beginning before dawn, and lasting up to an hour, from high up in the air. The habit has been overlooked, and points requiring further investigation are suggested, including whether any other species of Hirundinidae participate, or assemble in similar song-gatherings.

Williamson, K. (1950). The distraction behaviour of the Faeroe Snipe. *Ibis*, **92**, 66–74.

Field observations on lure display in *Capella gallinago faeroensis*, a comparison with that in *C. g. gallinago*, and a brief discussion on the nature and origin of such displays.

Williamson, K. (1951). Adult behaviour patterns occurring in the juvenile Oyster-catcher. *Brit. Birds*, **44**, 33–34.

Williamson, K. (1951). Aposematic behaviour of Snipe and Woodcock on being trapped. *Ibis*, **93**, 306–307.

A Snipe, probably *Capella gallinago faeroensis*, performed the full lure-display described by the writer for breeding birds (1950, *Ibis*, **92**, 66–74) in the laboratory on Fair Isle in October. From this he concludes that the lure-display pattern may be of aposematic rather than epigamic origin.

7. REPORTS OF ORGANIZATIONS

Blundell's School Science Society (1953). *Magazine for 1951–1952*, **7**, 54 pp.

Contains reports on weather, bird ringing and records.

Blundell's School Science Society (1954). *Magazine for 1952–1953*, **8**, 38 pp.

Contains reports on weather, bird ringing and nest records, a list of the birds of the Culmstock area, and studies of the oak in the woodland community and of the circulation of nitrogen in the Grand Western Canal.

British Trust for Ornithology (1953). 19th Ann. Rep. 1952, 64 pp. (Secretary, 2 King Edward Street, Oxford, 2*s*. 6*d*.)

Progress reports on sample census of great crested grebe, black redstart enquiry (1951), birds of high level woodlands, breeding distribution and habitats of pied flycatcher, wintering of gulls in Britain, survey of breeding distribution, ringing scheme, and final report by D. Lack on the investigation of the food of birds at the Edward Grey Institute, 1947–52.

Devon Bird-watching and Preservation Society (1954). *Twenty-sixth Report, 1953*. 75 pp.

In addition to the usual classified bird notes, contains a note on black redstarts in the county during the year, a report on the breeding biology of the spotted flycatcher, the census of heronries, a report on the Chapel Wood sanctuary, and a report on monthly wildfowl counts.

Diver, C. (1953). The work of the Nature Conservancy. *S. East Nat.* **58**, 1–9.

A useful survey of the Conservancy's first few years by its first Director-General.

Fair Isle Bird Observatory Trust (1954). Annual Report, 1953. (Friends of Fair Isle, Edinburgh, 21*s*. per annum.)

The main work of the observatory is the study of bird migration, but it has also included bird weights, sampling of avian blood, ectoparasites and breeding biology.

Freshwater Biological Association (1952, 1953). *20th Ann. Rep.* 53 pp. (Director, The Ferry House, Ambleside, Westmorland. 2*s*. 6*d*.); *21st Ann. Rep.* 53 pp. (3*s*.).

Summary reports on investigations of the hydrology of Lake Windermere, the ephemerid population of Ford Wood Beck, caddis larvae in tarns and streams, the small Crustacea of weed beds, and some of the lake fish.

Lincolnshire Naturalists' Trust Ltd. (1953). *Bird Observatory and Field Research Station, Gibraltar Pt., Lincolnshire, Report for 1952*. 40 pp. (Hon. Sec., A. E. Smith, 51, West St., Alford, Lincs., 2*s*. 6*d*.)

Contains reports on birds observed and ringed, on ectoparasites of birds (G. B. Thompson), dragonflies (A. E. Smith), Lepidoptera (R. R. Cornwallis and A. E. Smith), Coleoptera (E. C. Riggall), Diptera (O. M. White), Arachnida (G. M. Whatmough) and intertidal fauna (M. R. Young).

Lundy Field Society (1954). *Seventh Annual Report, 1953.* 56 pp. (L. A. Harvey, University College, Exeter, 2*s.* 6*d.*)

Contains a systematic list of birds seen on Lundy in 1953, and reports on bird-ringing, work on nesting sea-birds, the Lapland bunting invasion in the autumn, bird ectoparasites, wild and feral mammals, freshwater biology, and the habitats of the bristle-tail *Petrobius maritimus*.

Natural History Society of King Edward VI Grammar School, Camp Hill, Birmingham (1954). Brown's Coppice: a survey. pp. 80. 5*s.*

An admirable production for a school natural history society, consisting of a thorough survey of an area of 130 acres near Solihull, Warwickshire, including woodland, bog, and farmland. The animal groups studied included Protozoa, Coelenterata, Nematoda, Rotifera, Gastropoda, Annelida, Crustacea, Insecta (ten orders), and Vertebrata.

Norfolk Naturalists' Trust and Norfolk & Norwich Naturalists' Society (1954). *The Norfolk Bird Report, no. 1, 1953.* 51 pp.

Contains notes on breeding birds from five bird reserves in Norfolk and from Scroby Sands off Great Yarmouth, a short report on the year's work at Cley Bird Observatory, and a systematic list of the more unusual birds seen in the county during the year.

J. Northamptons. Nat. Hist. Soc. Fld. Cl. 32, 187–225, 1953. (A. E. Tyrrell, 179, Birchfield Road East, Northampton, 6*s.* 6*d.*)

Contains ornithological records and meteorological observations for the county, during 1952.

Oundle School Natural History Society (1954). *Annual Report, 1953.* 37 pp.

Contains reports on mammals, birds, bird-ringing, fishes, Crustacea, Opiliones, Lepidoptera, Ephemeroptera, Hemiptera, Diptera and Hirudinea in the Oundle district of Northamptonshire.

Society for the Promotion of Nature Reserves (1954). *Handbook, 1953.* 48 pp. (Brit. Mus. Nat. Hist., 5*s.*)

Summary reports on the reserves maintained by the society, and of the society's work and relations with the Nature Conservancy and the International Union for the Protection of Nature.

Rooke, K. B. (1953). Report on Dorset birds, 1952. *Proc. Dorset Nat. Hist. Fld Cl.* **74,** 133–148.

An annotated species list for Dorset with emphasis on migration; comparative notes from Portland Bill and St Aldham's Head.

Skokholm Bird Observatory Report for 1953 (1954).

Contains lists of the birds and Lepidoptera seen, and on the weather and migration, homing experiments with Manx shearwaters, and the effects of sea-bird manure.

Taunton Sch. Nat. Hist. Soc. Ann. Rep. 1952, 1–16.

Contains lists of fishes, amphibians, reptiles and moths (including light trap records) of the district.

Yorkshire Naturalists' Union (Vertebrate Section) (1954). Ornithology Division Report for 1953. *Naturalist,* pp. 47–72.

Gives the usual account of the bird observatories as well as dealing with the systematic list of birds.

REVENUE ACCOUNT FOR THE YEAR ENDED 31 DECEMBER 1954

Income

1953		£ s. d.	£ s. d.
	Subscriptions received, including arrears, and *less* payments in advance:		
545	Members taking *Journal of Ecology* only	578 10 4	
290	Members taking *Journal of Animal Ecology* only ...	313 8 8	
306	Members taking both Journals	341 3 11	
4	Associates	3 7 6	
1145			1236 10 5
102	Interest on Investments	108 15 0	
12	Interest on Deposit Account	13 7 6	
91	Interest on P.O. Savings Account	93 5 6	
205			215 8 0
38	*Journal of Ecology*, sales *less* costs		– – –
11	*Journal of Ecology*, Index to Vols. 1–20: Sales ...	11 0 0	
1	*Less* costs ...	1 6 9	
10			9 13 3
1	*Watson's Census Catalogue of British Lichens*: Sales ...		3 5 0
1399			£1464 16 8
	Journal of Ecology:		
1548	Sales: Current Volume 42		1623 0 10
738	Back Volumes and Parts		446 2 4
128	Reprints of Papers		145 9 10
11	Advertising space		15 2 4
	Contribution to cost of plates		20 0 0
	Balance		733 16 0
2425			£2983 11 4
	Journal of Animal Ecology:		
998	Sales: Current Volume		1080 14 4
716	Back volumes and Parts		643 13 9
82	Reprints of Papers		100 4 9
466	Balance		36 12 11

Expenditure

1953		£ s. d.	£ s. d.
	Working Expenses:		
30	Expenses of meetings	47 18 0	
27	Clerical assistance	6 11 0	
13	Audit fee	12 12 0	
11	Postages, etc.	13 2 4	
8	Printing and stationery	16 18 0	
6	Travelling	16 6 10	
3	Addressograph, stencils etc.	2 8 9	
2	Telephone	1 6 9	
—	Bank charges	11 4	
100			117 15 0
	Grants:		
10	Freshwater Biological Association	10 0 0	
—	British Co-ordinating Committee for Nature Conservation	2 2 0	
140	*Watson's Census Catalogue*	– – –	
150			12 2 0
	Journal of Ecology:		
—	Costs *less* Sales		733 16 0
	Journal of Animal Ecology:		
466	Costs *less* Sales		36 12 11
	Biological Flora of British Isles:		
118	Costs	298 12 10	
9	*Less* Sales	65 15 11	
109			232 16 11
574	Balance, surplus for year		331 13 10
1399			£1464 16 8
	Journal of Ecology:		
2013	Costs: Printing, Paper, Blocks and Binding ...		2599 14 5
287	Publisher's Commission		268 5 2
76	Carriage, etc.		109 1 11
6	Insurance of stock		4 14 4
4	Editor's expenses		1 5 6
1	Miscellaneous expenses		10 0
38	Balance		– – –
2425			£2983 11 4
	Journal of Animal Ecology		
	Costs: Printing, Paper, Blocks and Binding:		
267*	Vol. 23, No. 1	740 0 10	
1696	Current Vol. 23, No. 2	794 15 5	
1963			1534 16 3
209	Publisher's Commission		213 10 3
52	Carriage		54 1 3
20	Fee for checking references		20 0 0
14	Insurance of stock		13 15 6
4	Editor's expenses		6 0 8
—	Miscellaneous expenses		19 1 10
2869			£1861 5 9

BALANCE SHEET AT 31 DECEMBER 1954

Assets

	£ s. d.	£ s. d.
Cash in hand at Westminster Bank:		
Current Account	1216 0 6	
Deposit Account	1000 0 0	
		2216 0 6
Post Office Savings Bank Account		3824 11 4
Sundry payments in advance		3 18 9
Investments at Cost:		
£1200 of 3½% War Loan Stock	1230 4 1	
£700 of 3% Savings Bonds 1960/70	700 0 0	
£300 of 3% Savings Bonds 1965/75	300 0 0	
£1000 of 3% Redemption Stock 1986/96	1005 18 6	
		3236 2 7
		£9280 13 2

VICTOR S. SUMMERHAYES
C. E. HUBBARD
Hon. Treasurers

Liabilities

	£ s. d.	£ s. d.
Members' Subscriptions prepaid for 1955/57		47 12 7
Library Fund		1 5 0
Printing Accounts owing to Cambridge University Press:		
Journal of Animal Ecology		744 1 5
Sundry Accounts owing:		
Postage	4 14 6	
Stationery	1 8 0	
Addressograph	1 0 9	
Editorial Expenses	1 5 6	
		8 8 9
General Revenue Account—Surplus in hand:		
Balance at 31 December 1953	8147 11 7	
Surplus for year 1954	331 13 10	
		8479 5 5
		£9280 13 2

We have examined the Balance Sheet and Income and Expenditure Accounts of the British Ecological Society as at 31 December 1954, set forth above. We have obtained all the information and explanations we have required, and have verified the investments and Balance at Bank. In our opinion the above Balance Sheet is properly drawn up as to exhibit a true and correct view of the state of the Society's affairs, according to the best of our information and the explanations given us, and as shown by the books of the Society.

RYLAND CLIFT & NEAL.
Incorporated Accountants

10 ECCLESTON PLACE,
WESTMINSTER, S.W.1
15 *March* 1955

NOTICE TO CONTRIBUTORS

Contributors are asked to study these notes with care in order to save themselves and the editor unnecessary work in the revision of manuscripts.

1. All correspondence should be addressed: **The Editor, Journal of Animal Ecology, The Ferry House, Ambleside, Westmorland.**

2. TEXT. MSS should be typed double-spaced on one side of the paper, leaving top and left-hand margins at least an inch wide. Latin names of genera and species, **but nothing else,** should be underlined. Months of the year should be abbreviated (Jan., Feb., etc.) not indicated by figures. Text-figures are to be referred to as 'Fig. 1' etc. In the use of symbols, signs and abbreviations *British Standard 1991: Part I: 1954* should be followed, including the omission of all unnecessary full stops.

The *Journal's* conventions regarding cross-headings should be followed, but they should not be used too freely, **nor should headings be underlined.** Only long papers need include a table of contents. The Royal Society's *General notes on the preparation of scientific papers* should be followed on points not mentioned here.

3. LATIN NAMES. Excepting those of British vertebrates, all Latin specific names should be followed by the authority when the name is first mentioned in the text or tables. Names must be verified either from a standard list such as Kloet and Hincks's *Check-List of British Insects* or by submitting the final MS to the experts who have supplied the identifications.

4. REFERENCES should be listed in alphabetical order at the end of the paper in the form:

Vevers, H. G. & Fisher, J. (1938). The 1938 census of gannets (*Sula bassana*) on Ailsa Craig. *J. Anim. Ecol.* **7**, 303–4.

Titles of journals should be abbreviated according to the *World List of Scientific Periodicals*, except that the English usage of capitals for adjectives should be followed. Any reference not personally seen should be marked with an asterisk. **Nothing** except Latin names of genera and species should be underlined, nor should titles of papers or books be put in inverted commas.

5. TABLES should be set out on separate sheets and numbered in arabic numerals. So far as possible sufficient description should be included in the headings to make tables self-explanatory. The layout of tables should be kept as simple as possible; they are not printed 'boxed'.

6. TEXT-FIGURES. Drawings should be in jet-black indian ink, preferably on Bristol board. Shading must consist of lines or dots, not of half-tone washes. If the addition of mechanical stippling or hatching is required the area should be indicated by hatching lightly in blue pencil. Drawings should be arranged or grouped so that after suitable reduction a figure about 5 in. wide results. Graphs should be drawn on paper ruled in blue or faint grey; axes and graduation marks must be drawn in indian ink. All lettering, numerals and arrows should be shown lightly in pencil for insertion in uniform style by the blockmaker. The author's name and the number of the figure should be written on the back of each. Legends for figures should be collected together at the end of the MS.

7. PLATES. Photographs will only be used to illustrate important points which cannot conveniently be shown in any other way. Unmounted, glossy, half-plate prints showing good detail and moderate, but not excessive, contrast, are required. They should be numbered separately from text-figures, and each print should bear on its back the number and the author's name.

8. PROOFS. Page-proofs only will be sent. They should be returned with the least possible delay, and the minimum of essential correction should be made. Authors are requested to pay particular attention to the checking of numerical matter, mathematical formulae, tables and lists of names.

9. REPRINTS. Authors are supplied with 50 reprints gratis. Additional copies may be purchased if ordered when the proofs are returned. Contributors from abroad should order when sending their MSS. Reprints are sent out about a month after publication.